PERMO-CARBONIFEROUS VERTEBRATES FROM NEW MEXICO

By

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AND

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PREFACE.

The present work includes a series of papers dealing with the Permo-Carboniferous deposits of north-central New Mexico and their vertebrate fauna, so far as known. By courtesy of the Carnegie Institution of Washington it is published as a part of the series (publications 55, 145, and 146) by E. C. Case, dealing with the fauna of the Permian beds of North America. It has seemed best to us to publish these results jointly in order, by mutual study, to avoid as far as possible any errors, misunderstandings, or discussions in literature. The material in each case was studied by the author whose name appears first in the caption and the description and figures were then referred to the other author for careful criticism and discussion. Both authors accept fully all responsibility for the contents of the different chapters, except where dissenting or supplementary notes are attached, signed by the individual author. In all bibliographical references to the contents of this work the names of the authors should be given in the order in which they appear over each chapter.

The chapter by Mr. M. G. Mehl was prepared under the direction of Dr. Williston and both he and Dr. Case accept responsibility for the statements and figures.

The material described was collected by a joint expedition headed by Drs. Williston and Case in Rio Arriba County, New Mexico, in the summer of 1911. The beds had been previously explored by Mr. David Baldwin, in 1878 and 1879, chiefly in the interest of Yale University. Mr. Paul C. Miller, of the University of Chicago, was one of the party and Prof. F. v. Huene, of the University of Tübingen, was our guest for a short time.

Several of the forms known from New Mexico have been described in part or wholly elsewhere and such descriptions are not repeated. References to these articles are given in the list and bibliography of the fauna.

E. C. Case.
S. W. Williston.

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By

E. C. CASE, S. W. WILLISTON, AND M. G. MEHL

CHAPTER I.

DESCRIPTION OF THE VERTEBRATE-BEARING BEDS OF NORTH-CENTRAL NEW MEXICO.

S. W. WILLISTON AND E. C. CASE.

The following description of the Permo-Carboniferous beds of New Mexico is a portion of a more extended article by the authors in the Journal of Geology, only such portions being repeated as bear upon the character of the beds and indicate the conditions under which the animals lived and were preserved.*

The regions explored were El Cobre Cañon, north of Abiquiu, and the exposures in the walls of the Puerco and Gallina Rivers, all in Rio Arriba County.

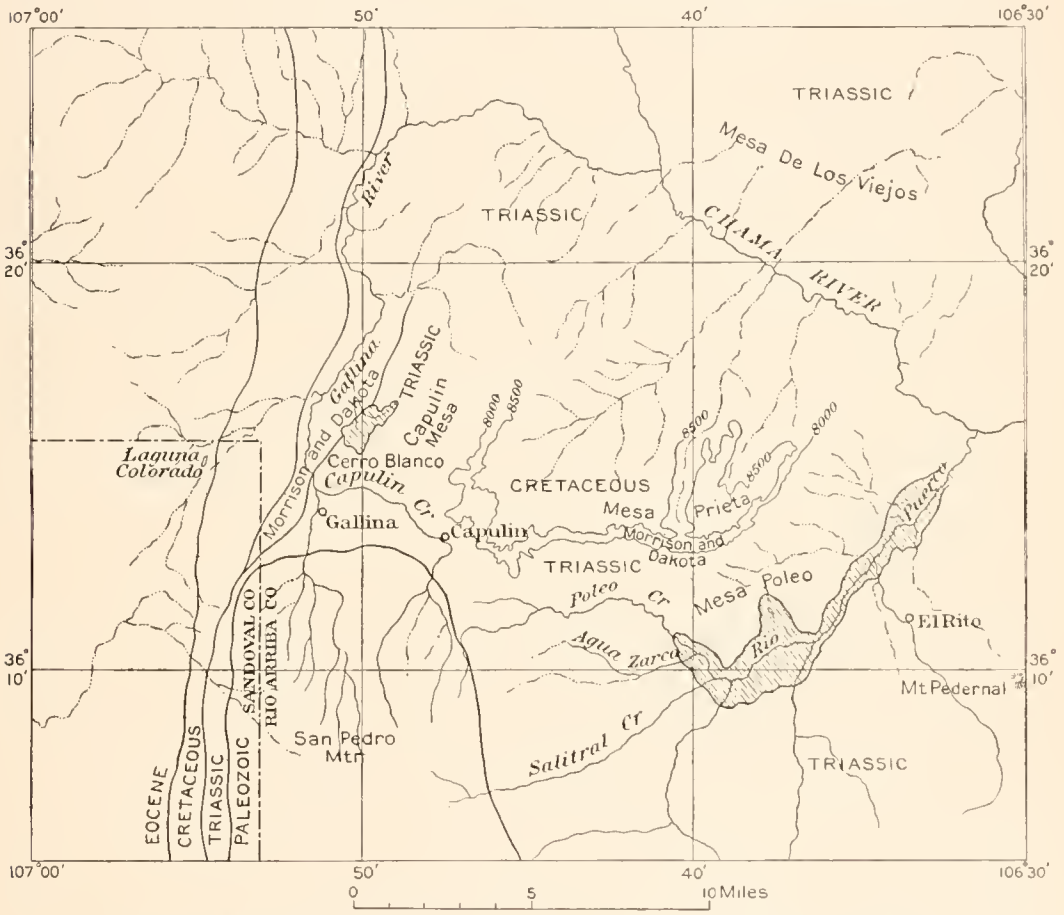

FIG. 1.—Map of the Mesa Prieta and adjoining country. Fossiliferous Permo-Carboniferous areas shown by shading. Comparison with the Gallina topographic sheet will make details clear.

El Cobre Cañon or basin is formed by the erosion of an unsymmetrical dome-shaped anticline, more or less faulted on the northeastern and southeastern sides, the brim formed everywhere by the massive sandstones of basal Upper Triassic age, the strata sloping in all directions, but chiefly east and west. The basin thus

* The Permo-Carboniferous of northern New Mexico. Journal of Geology, vol. XX, No. 1, pp. 1–12.

formed is about 2.5 miles in its greatest extent, in a north-and-south direction. Its very steep walls, for the most part about 700 feet in altitude, attain their greatest height in the northwest part, where the altitude may exceed 800 feet and where the Permian exposures are the greatest.

The erosion of the floor of this basin, acting on the beds of alternating sandstones and clays, has formed a series of steps or low cliffs, which for the most part dip at a small angle toward the west. Toward the sides and upper end of the cañon these ridges become more prominent, frequently forming high bluffs and cliffs. The lowermost beds in the cañon are deep chocolate-colored sandstones and fine conglomerates; the latter weather into low, rounded hills, frequently streaked with greenish layers. Bone fragments were found in these layers in various places in the basin. Above these darker colored sandstones are more massive sandstones, weathering more or less whitish, which ascend at the north end of the cañon to perhaps 350 feet above the stream bed. All vertebrate fossils that we found, of Permian or Permo-Carboniferous age, were below these sandstones, which form a fairly definite horizon about the basin and which may be taken as the lower limits of the Trias.

It has been questioned by us elsewhere whether the vertebrate fossils found in Texas, Oklahoma, southern Kansas, Illinois, and Pennsylvania are really of Permian age. At the south side of the cañon Case found a perfect cast of a *Spirifer*, identified by Professor Schuchert as *S. rockymontanus* Marcou, a form occurring in Colorado in the Pennsylvanian. Though the specimen was found free, so that its exact horizon could not be determined, its excellent preservation proves conclusively that it had not been carried far from its original bed, and inasmuch as vertebrate fossils are found in the deepest strata of the cañon it seems quite certain that the specimen came from an intercalated bed among those yielding so-called Permian vertebrates. No other explanation seems possible. It is the conviction of both the present authors that the lowermost at least of the strata yielding vertebrate fossils are of Pennsylvanian age, and this conviction is strengthened by the known position of the vertebrate horizons in Texas, Kansas, Illinois, and Pennsylvania, that of the last-named region being definitely known to be Pennsylvanian.

SECTION I. EL COBRE CAÑON.

	Feet.		
Yellow sandstone and conglomerates	75	Upper Trias	
Purplish and gray clays	40	?	
Purplish sandstones	20	Lower Trias?	Barren
Purplish clays and nodular sandstone	25	"	"
Red sandstone	5	"	"
Bright red clay	35	"	"
Purple clay	12	"	"
Bright red sandstones	22	"	"
Coarse purplish sandstones	12	"	"
Bright red clay with greenish nodules and purplish bands	100	"	"
Coarse, hard purplish sandstone	8	"	"
Bright red clay and sandstone	65	"	"
Hard red and purplish sandstone	6	"	"
Bright red sandy clay, with purplish streaks	90	"	"
Purplish and dark brown clay	22	"	"
Red clay and hard red sandstone	30	"	"
Hard purplish sandstones	35	"	"
Red clay	7	?	
Purple sandstones	3	?	
Red clay	22	?	
Permo-Carboniferous red and brown sandstones and clays, fossiliferous			

A section of the west wall of El Cobre Cañon, as far down as the horizons yielding fossils of Paleozoic age, is given above. It must be especially remembered, however, that this and Section II, on p. 4, will not apply in detail to any

other place, since it has been our experience in the Red Beds that detailed sections made in any given place can not be depended upon perhaps a quarter of a mile away. The top of this section, as already stated, yields vertebrate fossils of Upper Triassic age, and some of the Triassic vertebrates described by Cope from New Mexico came from El Cobre Cañon.

A survey of the surrounding country from the summit here, as also from the Piedra Lumbre, shows everywhere these basal Upper Triassic rocks as the lower or lowermost exposures.

From El Cobre Cañon the expedition turned westward on the Chama to the mouth of Cañones Creek, and then southwest across the Piedra Lumbre Mesa to El Rito ("branch") of the Puerco. The top of this mesa is formed of rocks of Upper Triassic age, and near the base of Mount Pedernal, which rises several hundred feet above the mesa, appears for the first time the heavy layer of gypsum marking the upper limits of the Red Beds, or so-called Trias. From the top of this mesa a good view of the adjacent country is afforded. To the north is the Mesa de los Viejos, with the Chama apparently occupying a fault line between, and the Arroyo Seco in

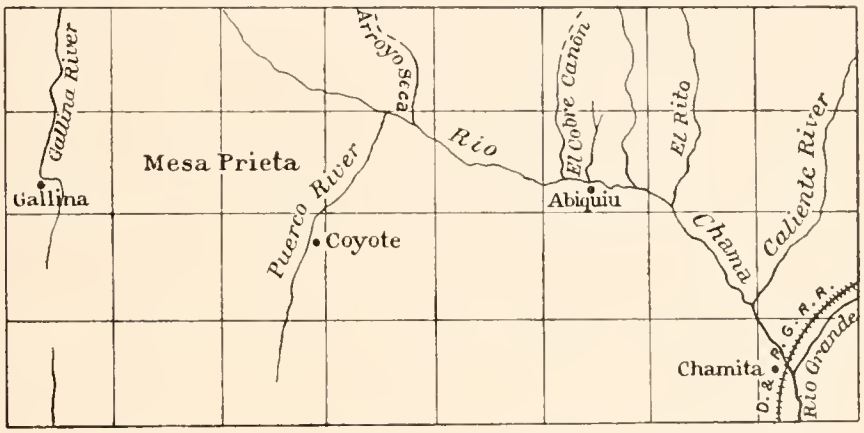

FIG. 2.—Map of region around Abiquiu, showing location of El Cobre Cañon.

a valley formed by the basal Upper Trias rocks sloping from the brim of El Cobre Cañon on the east and the superincumbent Triassic rocks on the west. To the west lie the Mesa Prieta and the smaller Capulin Mesa, separated by the Puerco, Chama, and Capulin, streams whose courses seem to have been influenced strongly by the faulting and dipping of the Trias.

The Puerco, to the mouth of the Poleo, has cut down into Permian strata, which attain their greatest exposure on the Poleo about a mile from its mouth. Our first camp was made on the Poleo (Arroyo de Agua), about a mile above its confluence with the Puerco.* Near the junction of the two creeks is a steep-walled cliff of Permian rocks about 100 feet in height, with a more or less flat table-land above it, a mile or so in extent, separating it from the Trias above. Farther west, where the Permian rocks find their greatest exposure, and where the Baldwin quarry lies, from which so many of the fossils in the Yale collection came, the very steep bluffs, in many places so steep as to be unclimbable, are about 700 feet in height. They are composed of alternating red sandstones and clays, with white and purple sandstones, clays, and conglomerates at the upper part, corresponding

* This Puerco Creek is not the one which gave origin to the name of the Puerco formation. The formation name was derived from a stream by the same name farther to the southwest.

quite to the massive sandstones forming the brim of El Cobre Cañon and the top of the Mesa Poleo, dipping northward to the foot of the Mesa Prieta. Phytosaur bones were found at the base of this white sandstone and in the pebbly conglomerates immediately underlying them. Permian fossils were found only in the lowermost 300 feet of these exposures, the intervening 300 feet of more or less vertical red clays and sandstones here, as everywhere else in the Rocky Mountain region, being quite barren. These rocks lie here, as elsewhere, apparently quite conformable with the superincumbent and subjacent beds, and doubtless represent the Lower Trias and perhaps more or less of the Upper Permian. The section of the bluff herewith given was made opposite our first camp on the Poleo, about a mile from the mouth of the creek; as is the case with the section at El Cobre, it can be depended upon only for a short distance on either side; the strata often change abruptly from sandstones to clays and vice versa.

On the north side of the adjacent valley of the Poleo the strata dip northward to the walls of the Mesa Prieta; just south of the creek they dip abruptly southward. About 2 miles above the mouth of the creek the beds bend down sharply and disappear beneath the alluvial deposits of the creek bed, doubtless indicating the line of a fault. Beyond this point the walls of the Mesa Prieta, formed exclusively of Upper Triassic and superincumbent beds, descend to the adjacent valley of the Poleo and Capulin creeks.

The Mesa Prieta rises about 1,500 feet above the beds of the Poleo and Capulin. Near the middle of the bluffs, at about the 8,000-foot line, there is a heavy bed of gypsum, which is taken to be the upper limits of the Trias, though, as we have said, in the entire absence of all fossil remains through 400 feet of these beds at least, everywhere, their age is assumed simply from their color—evidence that is, to say the least, exceedingly dubious, the more so from the fact that there is no petrological distinction between the Trias and Permian. Above this gypsum layer are the brownish and purplish shales of the Jurassic* and the lighter-colored sandstones of the Cretaceous, all lying quite conformably with the Red Beds below.

SECTION II. POLEO CREEK.

	Feet.		
Gray sandstones, mostly even-grained with pebbly conglomerates and shales below. Phytosaurs	30	Upper Trias	
Softer gray sandstones, weathering into sand	30	?	
Sandy clay, with beds of thin black shale; plant remains, fossil wood	40	Upper Trias?	
Sandy clay, black and green	12	Lower Trias?	Barren
Purplish sandy clay	6	"	"
Coarse yellow sandstone	33	"	"
Loose gray sand	6	"	"
Green and purplish sandstones	3	"	"
Gray and purplish sandstones	12	"	"
Hard clay, variegated and jointed (cliffs)	3	"	"
Purplish sandstones and red clay	30	"	"
Loose white sand with beds of red clay	40	"	"
First red nodular layer	6	"	"
Soft fine-grained, light red sandstones, cross-bedded, forming tops of pyramids and cliffs	6	"	"
Soft fine-grained, light red sandstones, cross-bedded with lighter bands of pebbles	3	"	"
Second red nodular layer, with clay	3	"	"
Red clay	2	"	"
Coarse cross-bedded sandstones	6	"	"
Third red nodular layer	6	"	"
Red cross-bedded sandstones	12	Lower Trias?	Barren

* The beds immediately overlying the gypsum have been called Dakota by Darton (*Bull. U. S. G. S. No. 435*) and Shaler (*Bull. U. S. G. S. No. 315*. p. 262). We searched in these shales for fossils, but without success. Elsewhere the beds overlying the Trias are either the marine Sundance (Wyoming), the Hallopus beds (Cañon City, Colo.), Morrison (southern Wyoming), or Lower Cretaceous (Kansas).

SECTION II. POLEO CREEK—Continued.

	Feet.		
Dark red and green clay	3	Lower Trias?	Barren
Coarse red and green sandstones	17	"	"
Hard red sandstones, cliffs	3	"	"
Red sandstone and clay with thin band of harder sandstone	18	"	"
Hard, red, coarse sandstone	3	"	"
Red clay	35	"	"
Red sandstone, bluffs	23	Base (?) of Trias	
Red sandstone with thin seams of clay, reptile bones	18	Top (?) of Permian	
Red clay with thin nodular layers	55		
Dark red, coarse sandstones (cliffs)	6	Permian, fossiliferous	
Red sandy clay	35	"	
Dark red, coarse sandstone, jointed	18	"	
Red clay, even texture, vertical rain erosion	50	"	
Dark red clay	8	"	
Red shaly clay	17	"	
Heavy gray sandstones	25	"	
Red sandstones and clays	?	"	

About 1.5 miles beyond the little settlement called Capulin a stream flows into Capulin Creek from the north along the line of a fault which divides the Mesa Prieta from the Capulin Mesa. The strata of the Mesa Prieta at this point dip slightly northwest, but those of the Capulin Mesa dip east and northeast. The west face of the Capulin Mesa rises 1,000 feet or thereabouts above the valley of the Gallina River. Just north of the Cerro Blanco is a high red wall similar to that north of the Poleo Creek, the uppermost rocks bearing phytosaur remains. It is confidently believed that the lowermost exposures here are of Permian age, but no fossils were found.

There is a sharp break between the Capulin Mesa and the Cerro Blanco. The rocks of the latter dip sharply to the west and are overlain by the Jurassic shales and the Cretaceous sandstones and shales. At the foot of these Upper Triassic rocks, north of Cerro Blanco, and opposite the face of the Capulin Mesa bluff before referred to, were found various small fresh-water invertebrates, and bone fragments referred provisionally to the genus *Cœlophysis* Cope. The horizon of these remains can hardly be less than 100 feet above the basal Upper Trias sandstones, and in all probability the original types came from the immediate locality where the fragments were found by Case. The Cerro Blanco takes its name from the massive beds of white gypsum which cap it, descending steeply below the creek bed to the south and dipping to the west. From the top of the Cerro Blanco one can look miles to the north and west, and the view therefrom is a revelation to the geologist. To the east lie the mesas of more or less horizontal rocks of predominantly Upper Triassic age; to the west the strata are deeply tilted and eroded into valleys; a few miles farther west the beds of the Wasatch badlands lie horizontally upon the uptilted edges of the Mesozoic strata.

Upon the whole, the general features of the Red Beds in northern New Mexico, as in many places elsewhere, may be summarized as follows:

The Upper Trias rocks, about 600 feet in thickness, perhaps more, are predominantly softer and lighter colored, often orange colored, yellowish, and whitish, and more aeolian in character, with the upper or uppermost beds more or less gypsiferous. These beds, as in the Lander region, have basal sandstones, reddish or white, with conglomerate and clay layers below them yielding phytosaur and labyrinthodont bones (both types were found at El Rito), corresponding well with like vertebrates from the Keuper of Europe. Below these beds there are not less than 350 feet (in the Lander and Kansas regions perhaps 900 feet) of more uniform red sandstones and clay layers, usually weathering into more vertical bluffs, that are utterly barren of all fossils and supposed to be of Lower Triassic

and Upper Permian age. Below these and conformable with them, in New Mexico and probably elsewhere, are not less than 300 feet, probably more, of prevailing coarser and darker-colored, often brownish sandstones, and dark-colored clay beds, yielding vertebrate remains hitherto considered to be of Permian age, but which in all probability are in part at least of upper Pennsylvanian age.

LIST OF KNOWN VERTEBRATES FROM THE PERMO-CARBONIFEROUS BEDS OF NEW MEXICO.

PISCES. Shark, like *Pleuracanthus*.

AMPHIBIA.

Eryops (?) *reticulatus*. Cope, Am. Nat., vol. xv, p. 1020; Case, Pub. 146, Carnegie Institution of Washington, p. 30.

* *Eryops* (?) *grandis* Marsh. (*Ophiacodon grandis*) Marsh, Am. Jnl. Sc., vol. xv, p. 211. Williston (*Eryops grandis*), American Permian Vertebrates, Chicago, 1911, p. 10.

Aspidosaurus novomexicanus Williston. American Permian Vertebrates, Chicago, 1911, p. 12.

Platyhystrix rugosus Case. Case (*Ctenosaurus rugosus*), Bull. Am. Mus. Nat. Hist., vol. xxviii, p. 176. Williston (*Platyhystrix rugosus*), American Permian Vertebrates, Chicago, 1911, p. 135.

Chenoprosopus milleri Mehl.

Genus indet., a small unidentified humerus.

REPTILIA.

Diadectes (*Nothodon*†) *lentus* Marsh. Marsh (*Nothodon*), Am. Jnl. Sc., vol. xv, p. 410. Case (*Nothodon*), Publication No. 145, Carn. Inst. Washington, p. 30. Williston (*Nothodon*), American Permian Vertebrates, Chicago, p. 16. Case and Williston (*Diadectes lentus*), Am. Jnl. Sc., vol. xxxiii, p. 339.

Animasaurus carinatus Case and Williston. Am. Jnl. Sc., vol. xxxiii, p. 339.

Diasparactus zenos Case. Bull. Am. Mus. Nat. Hist., vol. xxviii, p. 174.

Elcobresaurus baldwini Case. Publication No. 55, Carn. Inst. Washington, pp. 28 and 89.

Arribasaurus navajovicus Case. (*Dimetrodon navajovicus*) Publication No. 55, Carn. Inst. Washington, pp. 56 and 137.

Ophiacodon mirus Marsh. Am. Jnl. Sc., vol. xv, p. 411. Baur and Case, Trans. Am. Phil. Soc., vol. xx, p. 5. Williston, American Permian Vertebrates, Chicago, 1911, p. 81.

Sphenacodon ferox Marsh. Am. Jnl. Sc., vol. xv, p. 410. Baur and Case, Trans. Am. Phil. Soc., vol. xx, p. 4. Case, Publication No. 55, Carn. Inst. Washington, p. 66. Williston, American Permian Vertebrates, Chicago, 1911, p. 78.

Edaphosaurus novomexicanus Williston and Case, sp. nov.

Scoliomus puercensis Williston and Case, gen. et sp. nov.

Limnoscelis paludis Williston. Am. Jnl. Sc., vol. xxxi, p. 378. *Idem*, vol. xxxiv, p. 457. American Permian Vertebrates, Chicago, 1911, p. 23.

The genera *Dimetrodon* and *Clepsydrops* previously determined from the New Mexican locality have not been confirmed by later work.

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* The reference of these two species to *Eryops* is in a measure provisional, as later studies indicate a closely allied but distinct genus.

† The characters of *Nothodon*, so far as they have been determined, are identical with those of *Diadectes*, but there is a very considerable possibility that the skeletal characters other than those of the skull, the only part known, may justify the original generic name.

CHAPTER II.

A DESCRIPTION OF ASPIDOSAURUS NOVOMEXICANUS WILLISTON.

By E. C. Case and S. W. Williston.

Very few fossils were found on the west side of the Puerco River opposite El Rito, but from a small lens of clay inclosed in a bed of sandstone Mr. Paul Miller collected several associated bones which prove upon preparation to be the skull, portions of the vertebral column and carapace, the scapulæ, femora, humeri, portions of the pelvis, and some parts of the smaller limb bones of an animal indistinguishable from *Aspidosaurus novomexicanus* Williston. The type of this species (No. 810 Yale University Museum) is only partially preserved and the identification of the present specimen may not be accurate, but the resemblance of the parts preserved, especially the skull, is so close that it seems best to use the earlier name, provisionally, until more material can be obtained.

The most striking thing about this fossil is the strong resemblance of the skull to that of *Cacops aspidephorous* Williston from Texas. Aside from the condition of the otic region, the two skulls are almost identical. The same can be said for the pelvis, the limb bones, and the vertebral column, aside from the dorsal armor; this last is apparently composed of a single row of plates formed by expansions of the neural spines, the typical condition for the family *Aspidosauridæ*. A fragment of detached armor accompanying the specimen seems to be composed of two plates to each vertebra, but as the fragment consists of the plates alone, this point is not absolutely certain. The plates do not lie in two vertical series, as in the *Dissorophidæ*, but on the same level. On two of a series of separate plates, each being one of a pair, there is a descending process evidently for attachment to a neural spine; the presence or absence of a descending process in the others can not be made out because of the condition of the specimen. The meaning of this peculiar arrangement is not evident. Perhaps, as suggested by Williston, the forms included in the families *Aspidosauridæ* and *Dissorophidæ* are more closely related than has been supposed and this form may be a connecting link. However, the separation of the two families is very definite and easily determined and it seems desirable to wait for more evidence before abandoning the distinction. It is possible that the plates may come from the caudal region or (less probable but still possible) they may belong to another animal; this last suggestion is strengthened by the extremely slender descending process, which is far too delicate to have been a part of any of the neural spines preserved.

The skull: There is a strong resemblance between this skull and that of *Cacops*, and this extends to all minor details if we except the condition of the otic region and the ridges which run posteriorly from the orbit. In *Cacops*, Williston described two ridges running back from the posterior inner corner of the orbit, inclosing a triangular space; in this specimen there is but one ridge, the upper. The posterior portion of the skull has been nearly perfectly preserved on the left side, but that of the right has been largely restored in plaster. Fortunately the ends of the tabulare bones and the quadrates are preserved on both sides and this renders it very certain that in this specimen the otic opening was a deep notch, not closed by a posterior bar of bone as in *Cacops* and *Dissorophus*. This determines the

position of the quadrate bone in the lower bar of the otic opening and shows that it did not form part of the posterior bar of the opening in *Cacops*.

A careful examination of the bones of the temporal region of the left side shows a series of lines, very certainly sutures, as they are different in character from cracks which accompany them, and as some of them show, for a short distance, the peculiar wavy form of sutures. The course of these sutures and the relations of the bones thus outlined are shown in fig. 3 A. Similarly the outlines of the maxillaries, the lachrymals, and the jugals can be made out. From the strong resemblance of the skull to that of *Cacops*, in other regards, it is probable that the general course of the sutures was the same as in that genus. The otic notch is widely open posteriorly and the surfaces of the bones bordering it are smooth; but the adjacent portions of the skull, both on the sides and the top, are marked by a fine sculpture and pitting.

On the lower surface of the skull (fig. 3 B) the bones have the same general form and relationships as described by Williston in *Cacops*. The occipital condyles are well formed and inclined sharply backwards and inwards. The basisphenoid

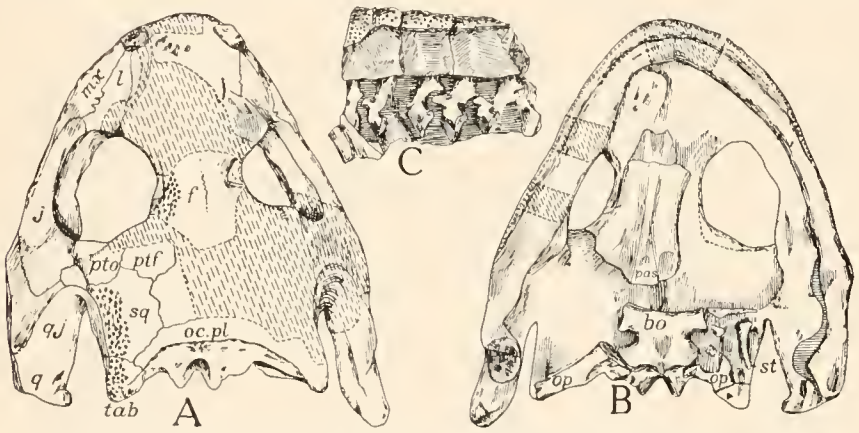

FIG. 3.—*Aspidosaurus novomexicanus*, No. 673, University of Chicago. × ½.
A, upper surface of skull, shaded parts restored; B, lower surface of skull;
C, three dorsal vertebræ with attached armor plates.

is well developed, with strong basipterygoid processes corresponding to the enlargement in the same position in *Cacops*. The basisphenoid was well ossified and evidently as fully functional as in the *Cotylosauria*. The ophisthotics are preserved, but the inner ends, perhaps due to injury, do not have the broad and fan-shaped form figured by Williston for *Cacops*. On the left side there is a slender styliform bone near the anterior end of the otic notch, which is without doubt the stapes, as it corresponds exactly in position with the same bone in *Cacops*. Anteriorly the large rhinencephalic chamber lies detached, by injury, from the basisphenoid, and on its lower surface lies the poorly developed parasphenoid. The lower jaws lie in position and most of the teeth are hidden, but a few in the right jaw and more in the maxillary show them to have been slender and conical; there is no evidence of any enlarged teeth, either in the upper or the lower jaws. The matrix and the lower jaws conceal the anterior portion of the palate, but so far as can be made out there is no trace of the large teeth which appear on the palate of *Cacops*.

The femora, humeri, scapulæ, and the *pelvis* (lacking only the crest of the ilium, as preserved) are indistinguishable from the same bones in *Cacops*.

The vertebræ are typically temnospondylous. There are three short series of vertebræ, one with the armor plates attached (fig. 3 c). In this the neural spines are short and heavy and the neural expansions are firmly attached to the spines; a careful microscopic examination of the broken surface reveals no trace of a suture or any interruption of the course of the bone fibers as preserved. The diapophyses are simple broad plates directed outward, with the single articular face directly slightly forward at the anterior end, as is common. There is no indication that the ribs were other than single-headed. In another short series of vertebræ the intercentra and the pleurocentra are preserved; the former are simple without any process for the rib, as in *Aspidosaurus glascocki* Case, but the condition is such that it is impossible to say whether there was a facet or not. The pleurocentra are small elements of indefinite form in the specimen.

There is a single detached fragment showing a series of armor plates, as mentioned above. This is bent upon itself so that at one end the ventral faces of the plates are in contact. The descending process of the anterior of the first pair of plates is very slender and could not have joined any of the vertebræ preserved. There is no descending process on the second plate. In the posterior plate there is also an indication of a descending plate, but this is less certain than in the first. If these plates came from the same animal as the vertebræ they can only have come from the caudal region, in which no plates occur in *Cacops* or in the Yale specimen of *Aspidosaurus novomexicanus;* if from another animal, they represent a form as yet undescribed.

A few poorly preserved phalanges show that the foot was broad and short.

CHAPTER III.

A DESCRIPTION OF CHENOPROSOPUS MILLERI, GEN. ET SP. NOV.

By Maurice G. Mehl.

The specimen herein described was discovered by Mr. Paul C. Miller, of the University of Chicago expedition, in 1911, on Poleo Creek, in the vicinity of Arroyo de Agua, northern New Mexico. It was found about 50 feet away from and approximately 2 feet below the skeleton of *Ophiacodon* Marsh described by Williston and Case in the following pages. The horizon is almost identical with that of the type specimens of *Ophiacodon* and *Sphenacodon* Marsh, collected by Mr. David Baldwin in 1878. The illustrations in this chapter were drawn by the author.

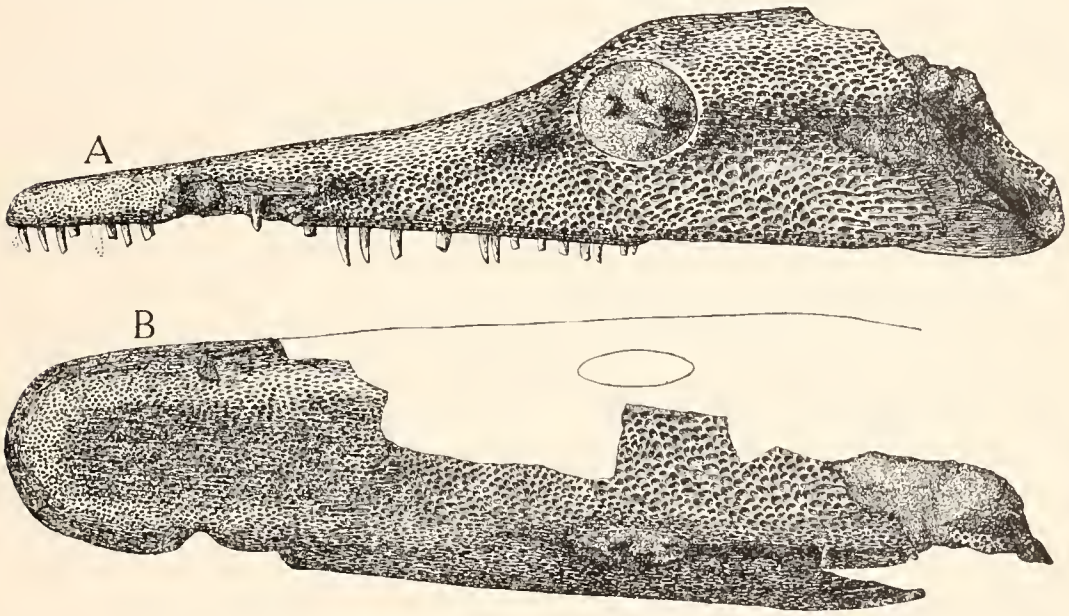

Fig. 4.—Skull of *Chenoprosopus milleri*, × ½. A, lateral view; B, dorsal view.

The material on which this genus and species is based consists of an incomplete skull. The anterior third and the left side, to the median line, are complete, with the exception of the loss of the upper posterior border of the skull, a little of the quadrato-jugal region, and a small portion about and including the left naris. Fragments from the right side were obtained, but they are so badly crushed and so incomplete that they are of little use other than in determining the position of the teeth. The specimen was inclosed in a hard sandstone matrix which, for the most part, was freed from the bone quite readily, leaving many of the sutures distinct and the pitting undisturbed. The skull is somewhat distorted and slightly compressed laterally. This distortion has cracked the surface and this, with the rather thorough ossification, has made the determination of some of the sutures extremely difficult. Only those that can be determined with certainty are shown in full lines, while the others are indicated by dots.

The *skull* is long and narrow, broadly rounded anteriorly, with the sides diverging slightly and regularly in the anterior four-fifths of the length. From this point the outline is slightly convergent. The greatest length of the specimen is about 288 mm. The width at a point 30 mm. back of the tip of the rostrum, the approximate length of the radius of the rounded anterior border, is about 54 mm. The greatest width of the skull was probably not over 90 mm. The sides rise abruptly to the plane of the table of the skull. In a lateral view the profile is triangular and low (fig. 4 A). The upper border of the anterior half is nearly straight and rises gradually from a height of about 13 mm. near the tip to about 33 mm. near the middle. From this point it rounds up gently in a concavo-convex curve to the horizontal plane extending over the posterior third of the skull. The greatest height is approximately 65 mm.

The *orbit* is nearly round and is about 32 mm. in diameter. The anterior border is a little back of the middle of the skull. The plane of the orbit is parallel with the lateral margin of the skull and is directed out and slightly upward. No sclerotic plates are present. The naris, which has a rounded anterior border and is straight behind, is about 10 mm. wide and 7 mm. long. It is placed near the lateral margin of the skull, about 50 mm. behind the tip of the rostrum. Its plane is directed out and upward. No pineal foramen has been observed. It is possible, however, that one was present, but slightly to the right of what seems to be the median line, and that it has been broken away in this specimen. From the middle of the posterior border of the orbit a depression extends back and slightly down for a short distance. A similar depression extends forward from the anterior border of the orbit and a third, somewhat smaller, lies a little behind the naris and in a line with the orbit and the naris. The dorsal surface (fig. 4 B) of the rostrum is slightly concave laterally from a point near the tip back nearly to the middle of the skull. The entire surface of the skull is marked with irregular pitting. In the upper posterior portion the pits are large and deep and are separated by irregular ridges. Anteriorly and below the pits become progressively smaller. Occasionally they run into each other to form antero-posterior grooves. This is especially true on the posterior end of the jugal. Here several lie parallel and are crowded close together. Extending back from the lower posterior corner of each naris is a smooth, shallow groove, evidently a mucus canal. The specimen probably belongs to an adult individual, for the ossification is so complete that no trace of suture is seen between the parietals or the frontals.

The *premaxillæ* are large and broad. They form the lateral boundaries of the nares as well as their anterior border. Their posterior border forms a concavity into which the nasals extend. The sutures bounding the *maxillæ* are uncertain, except for a short distance near the anterior end. From the narrow anterior extremity, which enters but slightly into the posterior border of the nares, they gradually broaden posteriorly to within a short distance of the orbit. From here they rapidly narrow to the posterior end, which apparently takes part slightly in the lower anterior border of the orbit. The extremity seems to be extended into an upper and a lower process that embrace the jugal. The teeth extend back to the middle of the orbit. Many of the teeth of the premaxillæ and the maxillæ are broken or wanting; still a fairly good idea of their size and number can be gained from those present; they are placed rather irregularly and show some variation in size. Apparently there is no arrangement according to size except that the posterior ones are all small. The variation in length and diameter is due, perhaps, to new teeth taking the place of those that have been lost. On each premaxilla there are 8 or more teeth and on each maxilla about 18, or between 52 and 56 in

all. They are all conical, slender, and more or less recurved. At the posterior end of the maxillæ there are a few that reach a length of only 4 mm. From this point they increase rapidly in length to an average of about 11 mm. At the base the cross-section of all is probably 3.5 mm. or less.

The *septomaxillæ* are small, triangular elements, fully twice as long as wide, and form nearly the entire posterior border of the nares. They extend back between the nasals and the maxillæ, but are apparently separated from the lachrymals by a considerable space. The *nasals* are large, rectangular in shape, about three times as long as wide. While the lateral boundary is not certain, the anterior half seems to be formed by the maxillæ and the posterior half by the lachrymals. Anteriorly, the nasals take part slightly in the inner posterior border of the nares, posteriorly they have a broad connection with the frontals and connect slightly; perhaps, with the prefrontals.

The *frontals* are long and narrow, being fully four times as long as wide. They extend nearly to the posterior border of the orbits. The anterior three-fifths of the lateral boundary is formed by the prefrontals and the postero-lateral border seems to be formed by the post-frontals. Lying about 25 mm. or 30 mm. behind the nares and between the nasals and the maxillæ there seems to be a long, narrow element, the *lachrymal*. To all appearances it takes part in neither the border of the nares nor that of the orbit. The posterior boundary is formed by the prefrontals and the maxillæ. The *prefrontal* is a triangular bone forming the entire anterior border of the orbit. Anteriorly it connects slightly with the nasals. The *postfrontal* forms the upper border of the orbit and apparently excludes the frontal from that opening by uniting with the prefrontal anteriorly. It extends back of the posterior border of the orbit some distance between the parietal and the postorbital. While the suture on the inner side is not certain the element seems to have but little lateral extent. The *parietal* is sub-rectangular, long and narrow. The posterior extremity is missing and its full extent can not be determined. Laterally it is bordered from the front backward by the postfrontal, postorbital, and supratemporal.

The *postorbital* is rather large, as wide as long, and forms the entire posterior border of the orbit. Immediately behind this and in contact with the parietal above lies a large rectangular element, probably the *supratemporal*. Bounding this below is a small portion of the *squamosal*, the lateral extent of which can not be determined, as the lower part is missing. At best, however, it must have been a comparatively small element. A small rounded notch, apparently the ear notch, separates the supratemporal and the squamosal for a short distance posteriorly. The *jugal* is a large element extending from the anterior border of the orbit back at least as far as the ear opening. It forms the lower posterior border of the orbit and increases somewhat in width posteriorly.

Unfortunately a complete knowledge of the region of the ear opening is prohibited by the condition of the specimen. When found the skull was broken through at this point and some of the bone was weathered from the exposed surfaces. The quadrate is present in the matrix, however, and serves to give some idea, at least, of this part of the skull. From the upper side of the quadrate a thin, plate-like bone extends up and forward in a direction as if to connect with the skull just above the ear notch. The outer edge is rough and pitted like the surface of the skull, while the posterior, incurved surface is smooth. The position of this process is such as to suggest its homology with the downward extension of the tabulare in *Cacops* Williston.* In that genus the tabulare extends back and downward to

* Williston, Bull. Geol. Soc. Am., vol. 21, p. 254.

fuse with the quadrate and thus completely close the ear notch. A thin plate of bone extends forward from the lower anterior inner edge of the tabulare and leaves but a small slit-like opening at the bottom of the large depression back of the ear notch. No such process is present in *Chenoprosopus milleri*, however, and the opening, if an opening, must have been considerably larger in the latter genus.

Little can be said of the palate; the anterior part is still inclosed in an extremely hard matrix, and although the left posterior part is exposed, the bones are somewhat crushed and their relations can not be told with any degree of certainty. The

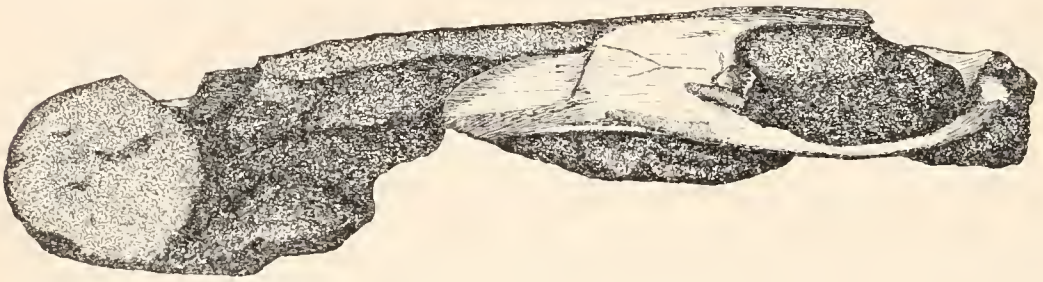

FIG. 5.—*Chenoprosopus milleri*, × ½. Palate view.

palate is essentially flat. The conjoined palatines and pterygoids are broad and leave a long, comparatively narrow inter-pterygoid opening. This is especially true in the posterior fourth of the palate, where the posterior processes of the pterygoids converge in a gentle curve inward to join the quadrate. In fact, unless the skull is compressed much more than the specimen would suggest, the opening at this point is a mere slit. The posterior pterygoid process extends upward in a thin plate, inclosing a large infra-temporal vacuity. This is approximately rectangular, about 65 mm. long and 35 mm. wide. The inner anterior border is broken, but suggests a postero-lateral process such as is seen in *Cacops*. While the parasphenoid is not preserved, one can say with some degree of certainty that its lateral extent was slight, because of the narrow inter-pterygoid space.

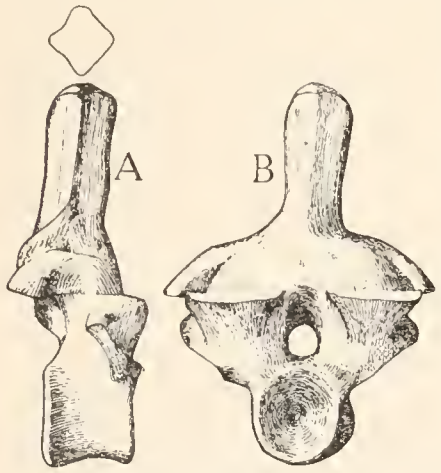

FIG. 6.—Diadectid vertebra, × ½. A, lateral view; B, anterior view.

Although the entire palate dentition can not be shown, some of the details are worth considering. Extending forward for a distance of about 40 mm. from the anterior border of the infra-temporal vacuity is a low rounded ridge, the posterior end of which is continuous with the inner border of the posterior process of the pterygoid. The anterior end curves outward slightly, away from the palate opening. This ridge is about 5 mm. wide and 3 mm. high and is closely studded with very fine tubercles. A similar ridge, but less pronounced, runs parallel to this on the outer side, at a distance of about 6 mm. It extends forward from the anterior border of the post-temporal vacuity for a distance of about 25 mm. This is also studded with the fine tubercles, as is the inner edge of the pterygoid to some extent. Along the lateral edge of the palate, running in a line parallel to the maxillary teeth at a distance of about 11 mm., are exposed four large teeth. These are spaced irregularly, the first about 60 mm. back from the tip of the rostrum and the

last near the middle of the skull or about 50 mm. in front of the anterior border of the post-temporal vacuity. Two are placed close together in the posterior, one of which is about 27 mm. in front of the last tooth in the series. Others are probably present but hidden by the matrix. They are stout, conical teeth, more or less recurved, averaging about 9 mm. at the base, and are about 19 mm. long. Cross-sections show their labyrinthine structure.

A single vertebra was found crushed into the palate of the specimen (fig. 6). The centrum is about 25 mm. in diameter and 24 mm. long. The general proportions and even the details are very similar to those of *Diadectes*, with the exception that the hyposphene of *Diadectes* is not present. From *Diasparactus* it apparently differs only in that the latter has a rounded, somewhat longer spine, while the present specimen has a quadrangular section with the diagonals directed antero-laterally and transversely and with somewhat concave sides. It is possible that the vertebra belongs to *Nothodon*. In short, it is distinctly of the Diadectid type.

To assign to *Chenoprosopus* a definite systematic position among the Permian vertebrates would be mere speculation at best, till more is known of the skeleton; but one is justified in considering the genus as belonging to the Temnospondyli, in spite of the fact that it has certain reptilian aspects. The vertebra found in association with the skull has all the appearances of that of a cotylosaurian, and its size and the amphibian nature of the skull show that the association must have been accidental and that the two could not belong to the same type. The narrow inter-pterygoid opening and the small parasphenoid that must have been present are not unknown among the Temnospondyli. In *Cacops*, while the inter-pterygoid space is wide, the parasphenoid is exceptionally narrow and in *Trematops* * it is vestigial or even wanting. Then, too, the irregular pitting of the skull, the probable mucus canals, and the large, conical teeth of the palate show its amphibian character.

Of the American Permian Amphibia, *Chenoprosopus* resembles *Cacops* most nearly, perhaps. It differs from *Cacops*, however, in the smaller nares, not only relatively but absolutely, and in their posterior position in *Chenoprosopus;* in the much narrower inter-pterygoid space of the latter, and in many minor points. The differences from *Trematops* are even greater: *Trematops* has an unpaired mucus canal or opening in the anterior part of the rostrum, large anterior nares confluent with the antorbital vacuities, and a wide palatal opening, none of which are present in *Chenoprosopus*. In general appearances the skull very much resembles that of the European *Archegosaurus*.† Both are comparatively long and tapering and in neither are the nares terminal. Even the arrangement of the cranial elements in the two forms, so far as it has been made out in *Chenoprosopus*, is similar. The posterior borders of the skulls, however, if the present interpretation of *Chenoprosopus* be correct, are very different. In *Archegosaurus* the border is indented by an otic notch, while in *Chenoprosopus* the posterior border is evidently formed by a bar that closes the ear notch, as described above. The wide inter-pterygoid space and the narrow pterygo-palatines of *Archegosaurus*‡ are also strikingly different from the condition found in *Chenoprosopus*. Besides these, there are many minor differences, such as the antero-posteriorly elongate nares and the more or less upward directed orbits of *Archegosaurus*, which are in contrast with the laterally directed orbits of *Chenoprosopus* and the nares that are

* Williston, Jour. Geol., vol. 17, No. 7, Oct.–Nov. 1909, p. 642.

† Jaekel, Zeitschr. d. d. Geol. Gesellsch., vol. 48, 1896.

‡ Credner.

slightly wider than long. In all probability a more complete knowledge of the form will show that the distinctive characteristics are of family value. (See fig. 7.)

The laterally directed orbits of *Chenoprosopus* are strongly suggestive of a terrestrial life. The sharp, conical teeth of the maxillaries and the tubercle-studded ridges on the posterior part of the palate would fit the animal admirably for feeding on the worms and the larvæ of the gigantic insects of its time.

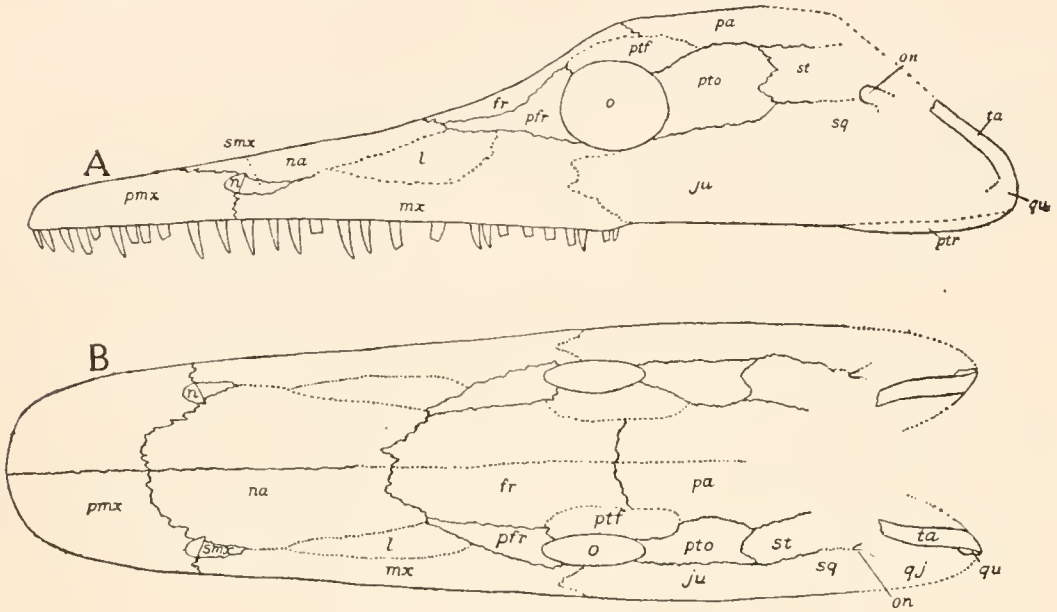

FIG. 7.—*Chenoprosopus milleri*, × ⅜.

A, outline of skull, lateral view: *pmx*, premaxilla; *smx*, septomaxilla; *na*, nasal; *mx*, maxilla; *l*, lachrymal; *fr*, frontal; *pfr*, prefrontal; *o*, orbit; *ptf*, postfrontal; *pto*, postorbital; *pa*, parietal; *ju*, jugal; *ptr*, pterygoid; *qu*, quadrate; *ta*, tabulare; *on*, otic notch; *st*, supratemporal (?); *sq*, squamosal.

B, dorsal view; lettering as in A.

The skull described above is No. 670 of the University of Chicago collections. The vertebra is No. 669. The writer is indebted to Dr. S. W. Williston for the privilege of studying this material and other specimens that are used for comparison and also for his kind suggestions and corrections in the preparation of this chapter.

CHAPTER IV.

DESCRIPTION OF A NEARLY COMPLETE SKELETON OF DIASPARACTUS ZENOS CASE.

By E. C. Case and S. W. Williston.

The specimen here described was found by Case in a reddish, clayey sandstone somewhat below the middle of the Permo-Carboniferous strata of El Cobre Cañon, in Rio Arriba County, New Mexico. When discovered, only a fragment of a tooth was exposed, but excavation revealed nearly the entire skeleton. As the skull was, unfortunately, near the surface, it is badly injured by weathering, and a portion of the upper surface was destroyed before fossilization, but enough remains to reveal by careful study most of the important characters. The atlantal and axial intercentra are preserved; the atlas is lost; the axis is preserved, but is separated from the rest of the vertebral column. Beginning with the third cervical, there is a series of five vertebræ in connection with the scapulæ, the clavicles, and the interclavicle. The posterior portion of the scapula of the left side is destroyed, but that of the right side, the clavicles of both sides, and the interclavicle, with the exception of the tip of the distal end, are perfect. Following the break between the sixth and the seventh vertebræ the series is complete to the twenty-third caudal. Though no fit can be found between the sixth and the seventh vertebræ the series was in position when excavated by Case and no reasonable doubt can be entertained that the relations are as described. This is borne out by the close relation which exists between the number of presacral vertebræ in this specimen and that found in other members of the same family, the Diadectidæ. The neural spines of many of the dorsal vertebræ and all but one of the caudals have been destroyed. The pelvis and the limb bones of both sides have been preserved in large part. The right ilium has lost the crest. All of the long bones of the limbs are preserved, but the carpus and tarsus and the phalanges of both sides have been more or less disturbed and many of the bones lost. Only a few of the ribs have been preserved, and only the base of a single chevron. No trace of abdominal ribs can be detected. This is in accord with the other specimens of this family recovered, where no trace of such structures has been seen, though they would certainly be expected.

In 1910 Case * described a short series of posterior dorsal and sacral vertebræ (Am. Mus. Nat. Hist. Cope Coll. No. 4794) from New Mexico and proposed the name *Diasaparactus zenos* to designate them. The posterior dorsal vertebræ of this specimen agree so closely with the described type that it seems best to retain the name for this specimen.

The weathered condition of portions of the specimen, the refractory nature of the matrix, in places, and the softer substance of the bones has rendered the preparation of the specimen very difficult, and it is to the painstaking care and skill of the preparator, Mr. Paul Miller, of the University of Chicago, that we owe our ability to describe the specimen so completely.

The *skull:* Lying close to the surface and being badly broken by weathering, the skull is imperfectly preserved and its study has been exceptionally difficult,

* Bull. Am. Mus. Nat. Hist., vol. xxviii, art. xvii, p. 174, 1910.

but enough has been made out to render certain the points here described. The top was destroyed previous to fossilization, so that it is impossible to give the exact height, but the length and width are correct within a few millimeters. In general the skull resembles that of the members of the family Diadectidæ. It may be best compared with the skulls of *Diadectes lentus* Marsh and *Animasaurus carinatus* described by us in the American Journal of Science.* It resembles the latter in the width of the posterior end, the narrowed occipital portion, and the fact that the posterior ends of the quadrates and the tips of the squamosal or tabulare bones are about on a line with the occipital condyle. It is also probable that the quadrates had the same backward and inward inclination of the outer faces as in *Animasaurus* rather than a position nearly parallel to the sides of the skull as in *Diadectes*. Other comparisons with the two genera are given in the description of the lower surface. The nares and orbits are similar in form and position to those of the other members of the family; the pineal foramen can not be made out, owing to the destruction of the upper part of the skull, but certain indications point to the fact that it had the same relatively large size. The outlines of the various bones of the skull can not be determined, owing to the condition of the surface.

The *maxillaries* have the usual form, semi-crescentic, on the ventral surface, with the concavity on the outer side. The alveolar surface is broad, accommodating the laterally expanded roots of the cheek teeth. Fourteen teeth are indicated in the maxillaries and premaxillaries, but as the last of the maxillary teeth is still somewhat expanded laterally, though smaller than the others, it is probable that there was a fifteenth tooth, small, conical, and almost rudimentary, as in *Diadectes*. This is the usual number in the family. The teeth of the premaxillaries were elongated and probably had chisel-shaped cutting edges, as in *Diadectes*, but as the incisor teeth of both the upper and lower jaws are badly weathered, only the central portion is preserved and this point may be in doubt. Some of the better-preserved ones seem to suggest a possibly conical form. The roots are very elongate, at least twice as long as the crowns. There is a distinct radial arrangement of the dentine around the pulp cavity, very clearly shown in several of the teeth. In none of the cheek teeth is the crown preserved, so that it is impossible to say more than that they were of the type common in the Diadectidæ.

The *posterior part of the skull* is preserved, in part, on the right side, showing the position and a part of the outer face of the quadrate. This bone was inclined so strongly inward that it looks even more backward than outward, resembling *Animasaurus* in this respect. The posterior edge of the quadrate is nearly flat and there is no trace of a quadrate foramen, but this may be due to the condition of the specimen. The prosquamosal reached down to the lower edge of the quadrate and then extended forward in a nearly horizontal line rather than rising somewhat abruptly, as in *Diadectes phaseolinus*.

The *lower surface of the skull* (fig. 8) shows the general form of the palate common in the diadectids, but combines characters of both *Diadectes* and *Animasaurus*.

Resemblances to *Animasaurus:* The anterior end of the palate narrows rapidly, due to the narrow muzzle; the prevomers and the anterior portion of the pterygoids are shown only by the broken edges, but it is apparent that they must have met in the median line and in all probability formed a high median keel which extended back to a small opening just anterior to the basisphenoid; the posterior end of the skull is broad across the quadrates, but narrowed in the occipital region;

* Am. Jnl. Sc., vol. XXXIII, April 1912, p. 339.

the quadrates are inclined backward and inward; the lower ends of the quadrates and the temporal or tabulare bones reach as far back, nearly, as the occipital condyle.

Resemblances to *Diadectes lentus:* The basisphenoid is broad and short instead of narrow and elongate as in *Animasaurus;* the articular faces of the quadrates are broad antero-posteriorly; in *Animasaurus* they are narrow.

In this specimen no trace can be found of the palatine processes of the maxillaries so characteristic of the family, but as the skull is poorly preserved and has been badly crushed it seems to us more probable that the processes have been injured beyond recognition than that they were absent.

The *lower jaw:* On the right side the articular portion is missing, but on the left side it is the posterior portion of the jaw which is preserved, so that the length and proportions of the jaws can be made out. It was less deep than in *Diadectes*, but in other respects very similar. There was a well-defined coronoid process and the usual two Meckelian openings on the inner side, the anterior one seemingly somewhat smaller than in *Diadectes*. The anterior end of the two jaws, in position, was narrower, corresponding to the narrowed muzzle. The broken condition of the specimen reveals the deep sockets of the incisor teeth and the roots of several teeth marked by the deep linear grooves due to the folding of the dentine. The articular surface of the articular bone shows two deep concave faces, which, in opposition to the corresponding prominences on the lower face of the quadrate, limited the motion of the jaws to a strictly vertical plane. As in the skull, the outlines of the individual bones can not be made out.

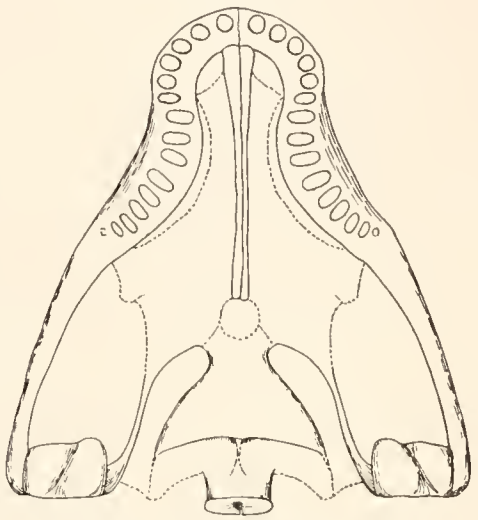

FIG. 8.—*Diasparactus zenos* Case, × ⅔. Restoration of lower surface of skull.

The *shoulder-girdle:* This, as is not uncommon in the specimens of the family, is well preserved and almost undistorted; this is due to its strength, the close articulation of the bones, and probably also to the presence of a considerable quantity of tough cartilage. The distal half of the right scapula, portions of the cleithra, and the tip of the posterior end of the interclavicle are wanting. In comparison with the scapula of *Diadectes*, the blade is shorter and the proximal portion wider. The posterior edge is more sharply curved, forming a semicircle. The lower, or inner, edge is straight in the middle, curving gently at the posterior end to join the posterior edge of the bone and more sharply at the anterior end to join the anterior edge. The anterior edge is nearly straight, with scarcely noticeable faces for the clavicle and cleithrum. The posterior edge is crescentic in outline, becoming more sharply curved toward the proximal end. On the outer face there is a prominent preglenoid tuberosity anterior to and above the humeral cotylus; posterior to it the edge of the bone is broad and bifurcates to include the supraglenoid fossa with, apparently, a supraglenoid foramen at its bottom. On the other, anterior, side of the tuberosity is a deep and wide opening, which terminates at the bottom in the supracoracoid foramen. Just beneath the preglenoid tuberosity and anterior to the articular surface is a very large, funnel-like foramen, the glenoid, which is the largest foramen observed by us in this position in any of the cotylosaurs. The articular surface has the usual two facets, the upper, anterior, facing

obliquely downward and slightly backward and the lower, posterior, facing obliquely upward and slightly forward. The inner surface of the scapula is hidden on both sides in large part, rendering it impossible to describe the subscapular fossa. It is impossible to trace any sutures between the bones, but both coracoids are surely present.

The *interclavicle:* This bone is very little expanded at the anterior end and is strongly united by deep sutures with the clavicles, resembling very closely in this respect the unnamed clavicles and interclavicle from Texas (No. 4390 Am. Mus. Nat. Hist. Cope Coll.) described by Case in Publication 145 of the Carnegie Institution of Washington, page 79, figure 26. The posterior portion of the interclavicle is nearly straight, gradually becoming narrower toward the posterior end, which is lost.

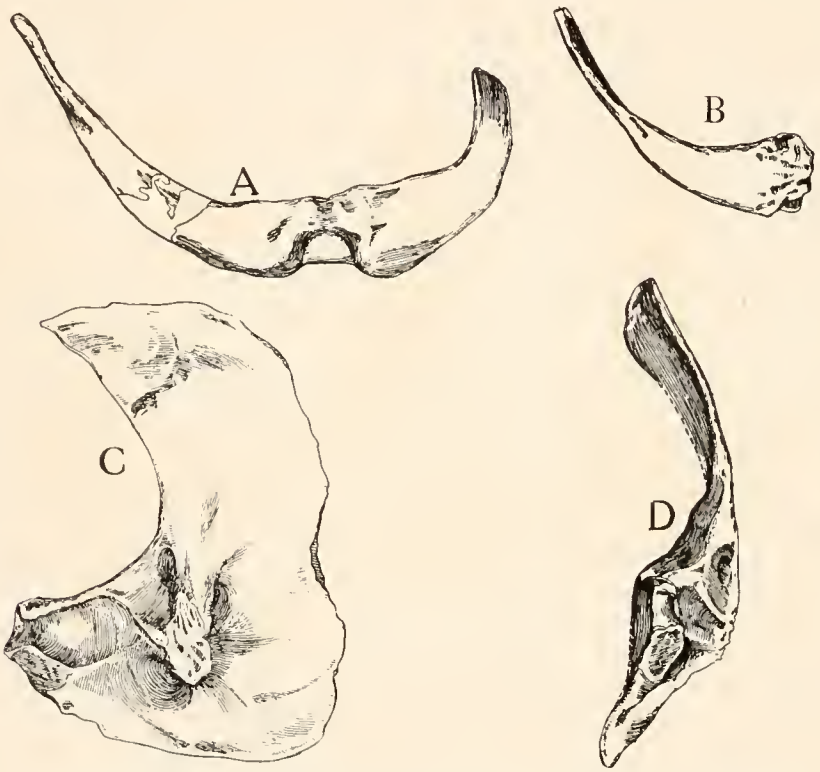

FIG. 9.—*Diasparactus zenos* Case, × ½. A, anterior view of clavicles and interclavicle; B, upper view of right clavicle; C, outer surface of right scapula; D, posterior view of right scapula.

The *clavicles:* These are very strong proximally and higher than the anterior end of the interclavicle. They join the sides of the interclavicle but meet behind it, so that there is a median depression or fossa between the proximal ends of the bones anteriorly. Seen from in front the proximal ends of the clavicles are broader than high, presenting a wide flat face to the anterior edge of the scapula. A few centimeters back the clavicles become suddenly flattened, so that they are very thin antero-posteriorly, in the natural position of the bones, but wide vertically; they continue in contact with the scapula for their full length. The distal ends of the bones become gradually contracted to narrow points.

The *cleithrum:* There is no trace of the cleithra attached to the scapulæ on either side, but there are two isolated fragments which appear to be portions of

the bones from the two sides. The posterior end of the bone was broad and thin and evidently applied to the outer face of the posterior end of the scapula. Anteriorly it contracted to a narrow, relatively short process, which was applied to the upper surface of the scapula or the distal end of the clavicle.

The *humerus:* The bone of the right side is perfect, but that of the left side has lost a small fragment from the upper border of the entepicondylar foramen. In general the form is the same as in *Diadectes phaseolinus*, but differs in some particulars. The proximal and distal ends have about the same inclination to each other as in *D. phaseolinus* and there is the same lack of any well-defined shaft. The articular face for the scapula is narrow and extends nearly parallel to the greatest length of the head of the humerus instead of obliquely across it, as in the pelycosaurs and some Cotylosauria. Near the inner end of this face is a deep, rather elongate pit, with a prominent lower border but open on the upper edge. Beyond this pit the end of the bone falls away sharply to the inner, deltoid, pro-

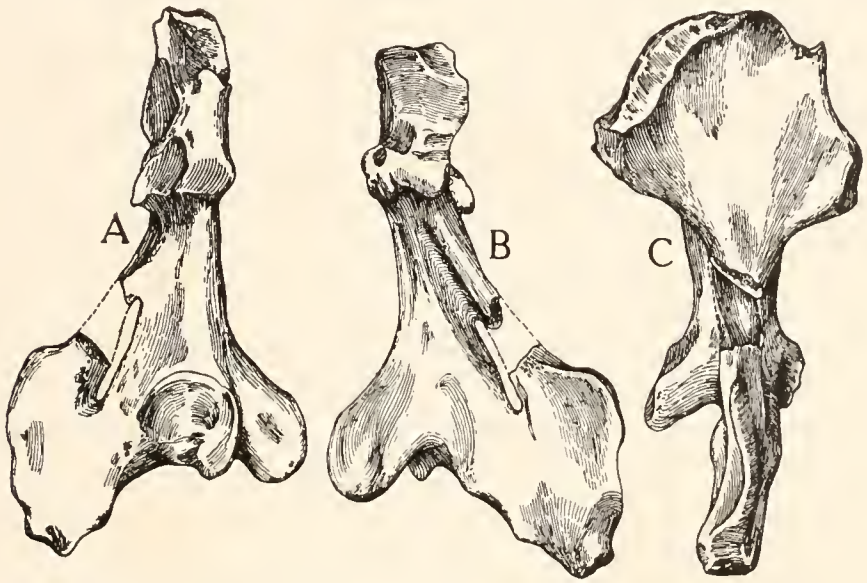

FIG. 10.—*Diasparactus zenos* Case, × ½. A, anterior surface of left humerus; B, posterior view of left humerus; C, view of inner side of left humerus.

cess, which extends almost directly outward and does not curve downward and inward toward the anterior face of the bone, and does not send an extension downward on the shaft, as in the pelycosaurs, nor even so much as in *D. phaseolinus*. On the extremity of this process is a well-marked pit for the attachment of a strong ligament. The process on the posterior side of the proximal end is fully as prominent as that on the anterior end.

In *D. phaseolinus* there is a strong process on the anterior, radial, edge of the shaft near its lower end, which extends almost directly outward, probably for the attachment of the supinator muscle; a similar process occurs in the same position in *Seymouria*, *Limnoscelis*, though small, and in *Sphenacodon* and *Dimetrodon*, and has been called the ectepicondylar process. In the amphibians *Eryops megacephalus*, *Trematops*, etc., there is a like process. In this genus there is no such process; the shaft of the left humerus is perfectly smooth at the position of the process, but on the right humerus there is a slightly elevated rugosity. In *D. phaseolinus* the distal end is relatively broader, the entocondylar process

is longer and higher, and the foramen is smaller. The humerus of the specimen of *D. phaseolinus*, with which this specimen was compared, is actually larger and the foramen actually smaller, increasing the relative difference. In this specimen the entocondylar process of the right humerus is slightly distorted, the upper edge running obliquely downward from the shaft to the lower end; but on the left humerus, which is undistorted, it passes out from the shaft more directly and there was a long, somewhat oblique, inner edge to the process. On the lower corner of this process there is a deep pit for the attachment of a ligament.

On the back of the bone directly opposite the articular surface for the radius is the strong ectocondyle, similar to that on the humerus of *D. phaseolinus*. The position and large size of the ectocondyle, directed prominently backward and even inward from the plane of the distal end, seem to be correlated with a powerful, thickset humerus, short fore-arms, short, flattened feet, and especially with non-acuminate ungual phalanges. It is the condition found in *Eryops* and *Trematops* among the amphibians, *Ophiacodon* among the pelycosaurs, *Limnoscelis*, *Diadectes*, *Diasparactus*, and *Seymouria* among the cotylosaurs. Williston found the digits more slender in *Seymouria*, but no indications of acuminate claws have been found in that genus. The great development of these processes for the attachment of the extensor and supinator muscles on the outer side, of the flexor muscles on the inner side, and the great mechanical advantage these muscles must have had, are certainly correlated with a powerful manus; but the structure of the arms and hands in the *Captorhinidæ* is like that of the more cursorial structure found in other pelycosaurs and cotylosaurs, and indicate widely different habits for this group of Cotylosauria.

The face for the radius is semicircular in form, with the lower, inner, border truncated; the articular surface is flat or even concave, indicating the presence of a large amount of cartilage and differing notably from the same face on the humerus of the pelycosaurs, where it is strongly convex. As the face has the same appearance on the bones from both sides it must be regarded as natural, but may be merely ontogenetic in character. The face for the ulna is elongate and oblique in position, passing from within outward and downward. It is largely confined to the distal end of the bone, appearing only slightly on the lower, anterior, face, and not at all on the upper, posterior.

The *ulna* resembles that of *D. phaseolinus*, but is proportionately longer and more slender, without such heavy extremities and without the accompanying rugosities. The shaft is wide but thin. The upper end has an oblique, nearly flat, slightly twisted, articular surface for the humerus; it was simply applied to the corresponding face of that bone and did not embrace it, as in the pelycosaurs. The lower end is a little expanded and presents two articular surfaces lying at less than a right angle to each other and not separated by any non-articular space. They are set at such an angle with the flat surface of the bone that they look more inward than directly downward. The distal end of the shaft is curved inward slightly at the lower part, increasing considerably the effect just mentioned. Viewed from the posterior edge, the bone has a slight but very evident sigmoid outline.

The *radius* is shorter and heavier than the ulna; the shaft is triangular in section, with the thicker portion on the ulnar side. The proximal end is expanded, with a semicircular face truncated on the posterior side. The articular surface is gently concave; this concave face opposed to the concave face on the humerus indicates the presence of a large amount of cartilage in the joint. The distal end is elongate laterally, but rather narrow antero-posteriorly. There are two faces; a short inner face, which, in connection with the oblique face on the inner side of

the distal end of the ulna, forms a notch into which the intermedium fitted, and a larger outer face, nearly horizontal and occupying most of the distal end.

The *carpus:* In no specimens of the Diadectidæ previously collected have more than a few of the bones of the carpus been preserved and in none are they in position. In this specimen most, if not all, of the carpal elements of the right side are in connection with the radius and ulna and some of the metacarpal bones, though somewhat disturbed by the bending of the foot backward and inward. The carpus of the left side is separated from the bones of the fore-arm and not all are preserved. Seven bones are clearly preserved on the right side and there are indications of two others. The bones of the proximal row and a centrale are large and well formed, but those of the distal row are reduced to small nodules and were

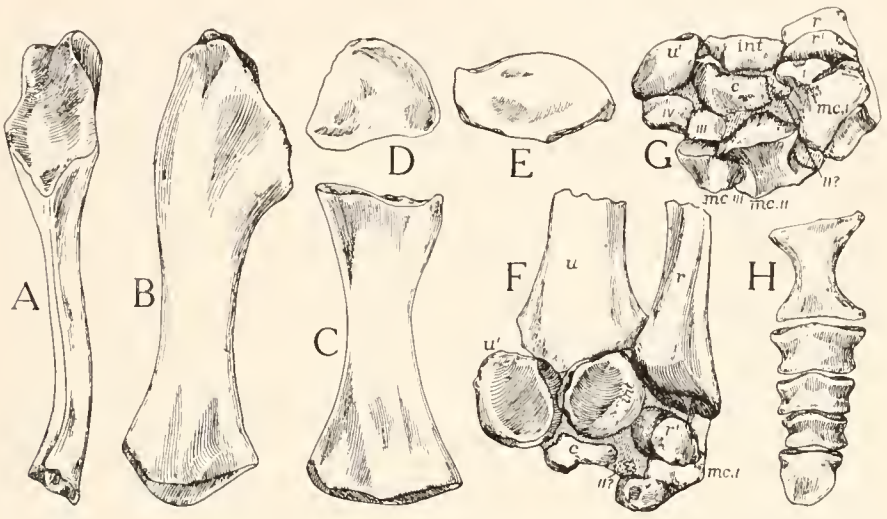

FIG. 11.—*Diasparactus zenos* Case, × ½. A, anterior view of left ulna; B, inner view of left ulna; C, anterior view of left radius; D, upper end of left radius; E, lower end of left radius; F, lower ends of right radius and ulna with carpals of proximal row, upper surface; G, carpals of distal row of right side with attached metacarpals, upper surface. This is the distal portion of the carpus shown in F, which is bent back upon itself; H, metacarpal and phalanges of third digit of right front foot.

evidently inclosed in a considerable amount of cartilage, resembling in this respect the foot of *Limnoscelis*, described by Williston.* The *ulnare* is roughly oval in shape, with broad articular faces for the intermedium, the ulna, and carpale IV. The outer edge is narrowed above, but widens below to form a triangular articular surface which probably afforded attachment to a pisiform, which is not preserved, however, in either carpus. The *intermedium* is thick and oval in outline; it articulated fairly closely in the notch formed by the adjacent faces of the radius and ulna, and touched the radiale, ulnare, and the centrale. The *radiale* is smaller, rather longer than wide, and lay along the larger, inner, facet of the radius. As in *Limnoscelis*, it was not large enough to articulate with this face for its whole length. The *centrale* is elongate with a flat lower face; the upper face is flat on the radial side, but near the ulnar end there is a sharp upward projection which fitted between the ulnare and the intermedium. On the radial end of this bone there is a small fragment partly inclosed in matrix which may indicate the second carpale. The bones of the distal row are all small and of indefinite form. One, of larger size, probably carpale IV, lies below the ulnare, a second below the ulnar end of

* Am. Jnl. Sc., vol. XXXI, May 1911, p. 390.

the centrale. None appears in the specimen directly beneath the centrale. Below the radiale is an uncertain fragment which appears to be the proximal end of the metacarpal with a first phalange attached to its lower end. On the inner side of the proximal end of this fragment is a small nodule which is apparently carpale I.

The distal portion of the foot was very broad and strong, with heavy, short phalanges. As neither of the fore feet is complete, it is impossible to give the phalangeal formula, but it is very probable that it was the usual reptilian number, 2, 3, 4, 5, 3. The metacarpals have very broad proximal and distal extremities, which narrow rapidly to a shaft not over half so wide as the ends. Viewed from the sides the extremities are wider than the shaft, but the difference is not nearly so great as in the horizontal view. The articular surfaces are flat. The phalanges are broad, short, and thin, with only a slight constriction of the sides to indicate a shaft. The articulations are better formed than in the metacarpals, as there are well-modeled concave and convex surfaces indicating a considerable freedom of motion. The shape of the articulations between the phalanges indicates the possibility of closing the hand, but also a considerable resistance to any bending back of the digits. The terminal phalanges are broad and oval; the proximal articulation with the adjacent phalange was close. The edges of the bone are thin, but there is a distinct thickening on the under side near the distal end and a distinct concavity of the lateral edges, indicating the attachment of a strong flattened claw or nail-like claw.

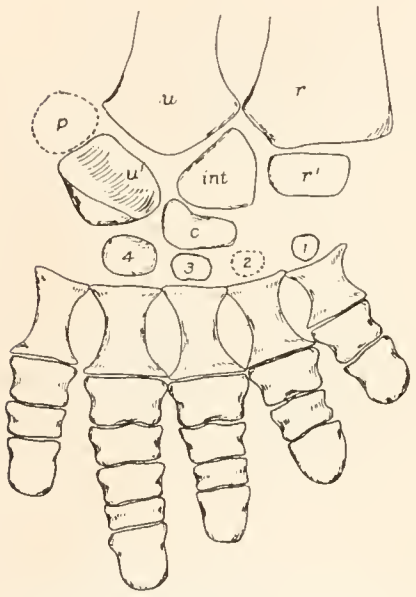

FIG. 12.—*Diasparactus zenos* Case. Restoration of right front foot. × ½.

The interpretation of this type of limbs and feet, so characteristic of some of the contemporary amphibians and most of the contemporary cotylosaurs, with the exception of the Captorhinidæ, has been in dispute. Abel accepts them as fossorial. Matthew, in a review of Abel's Paleobiologie (Science, March 1, 1912), expresses the opinion that the animals were aquatic in habit. From this conclusion we must enter our dissent. There is not a character shown in the Limnoscelidæ, Diadectidæ, or Seymouriidæ that could lend support to this hypothesis unless it be the imperfect ossification of the mesopodium. The structure of the body throughout is heavy; the tail is short and without propelling power, as indicated by the short spines and chevrons. The fingers are short and stumpy, with well-articulated phalanges and with the terminal ones clean-cut and provided with heavy nails or blunt claws, all of which would be out of place if their main function was the support of a swimming web. In most, if not all, aquatic reptiles and amphibians the foot is elongate with shapeless phalanges, not well articulated. Furthermore, it is quite certain from the natural articulations that the elbow was normally bent at an angle and it is very doubtful whether the fore-arm would have been extended fully in line with the humerus. Nor can we now believe, in opposition to views previously expressed by Case, that these animals were essentially fossorial in habit, since the short, though powerful, legs (in some forms at least) were not long enough to extend the hands in front of the head. It seems more probable that these animals, as well as the Eryopidæ, were marsh-dwelling creatures, doubtless living among the rank vegetation in the vicinity of water,

which they occasionally entered, but using the feet in digging and excavating for food. Invariably animals using the feet as propelling paddles have the propodials more or less elongated, while in tail-propelling animals not only the propodials but the epipodials are shortened and the digits elongated. In none of these groups will the cotylosaurs enter. Upon the whole it seems to us that the habits of these animals may have most nearly approximated the present habits of the marsh turtles.

The *pelvis* is very nearly perfect. The crest of the ilium of the left side is broken away and the median portion of the pubis is slightly injured, otherwise the bones of both sides are complete. As in the rest of the skeleton the nature of the bones makes it impossible to trace the sutures. The crest of the *ilium* is elongate antero-posteriorly, with the posterior end somewhat higher than the anterior, so that the upper line slants downward and forward. The upper edge is thin, but 2 or 3 centimeters below the crest there is a sudden thickening, forming a distinct shelf with a nearly horizontal upper surface. The posterior end is formed

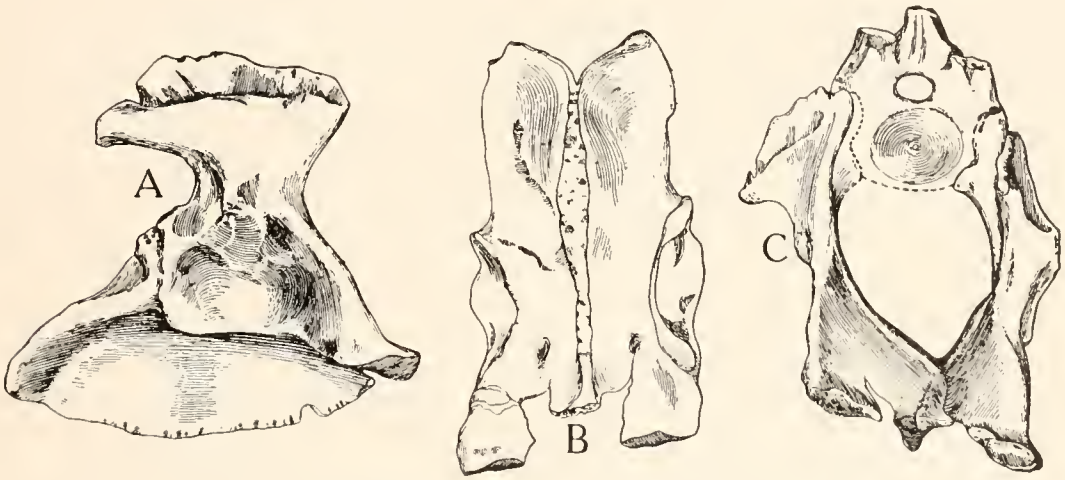

FIG. 13.—*Diasparactus zenos* Case, ×½. A, right side of pelvis; B, lower view of pelvis; C, anterior view of pelvis; face of sacral vertebra somewhat restored.

by a thickened process, about a centimeter wide, which is the direct continuation of the shelf mentioned. Below the shelf the ilium contracts rapidly until it is less than half as wide as the crest. The acetabulum is of the form common in the Cotylosauria, rather shallow and longer than high. The anterior edge is not well defined, but posteriorly there is an elevation of the rim on the proximal portion of the ischium forming a buttress for the head of the femur. Above, there is the usual tuberosity on the ilium at about the middle of the upper line of the cavity.

The *pubis* is shorter than the ischium. The anterior edge, opposite the acetabulum, is convex, but toward the lower end the edge becomes wider and the bone is turned so that it is nearly horizontal. The anterior end is thickened with an elongate, flat, oval face indicative of the presence of a prepubic bone as suggested by Broili. The lower portion of the bone is nearly flat (fig. 13 B), but towards the median line it is turned sharply down and, in union with the bone of the opposite side, forms a deep symphysis indicated on the outer surface by a prominent keel. The pubic foramen lies just below the anterior end of the acetabulum, it penetrates the bone directly, passing slightly upward and forward to open on the flat anterior face described below. Viewed from the front, the cavity of the pelvis is slightly

oval in outline, a little higher than wide, and the pubes present broad faces triangular in outline and slanting inward, downward, and forward, but the anterior ends of the bones are horizontal (fig. 13, c), so that at the base of the broad faces there is a flat shelf, perhaps slightly indented at the median line where the two bones meet.

The *ischium* is longer than the pubis, extending posterior to the acetabulum almost twice as far as that bone does anterior to it. The upper margin begins near the upper posterior edge of the acetabulum and runs backward and downward in a concave line. The posterior part of the margin turns downward and joins the posterior border in a sharp angle; this border is nearly straight and passes sharply inward, downward, and a little forward. The union of the bones of the two sides leaves a notch at the posterior end of the pelvis. As in the pubis, the main portion of the bones is horizontal below the acetabulum, but the inner

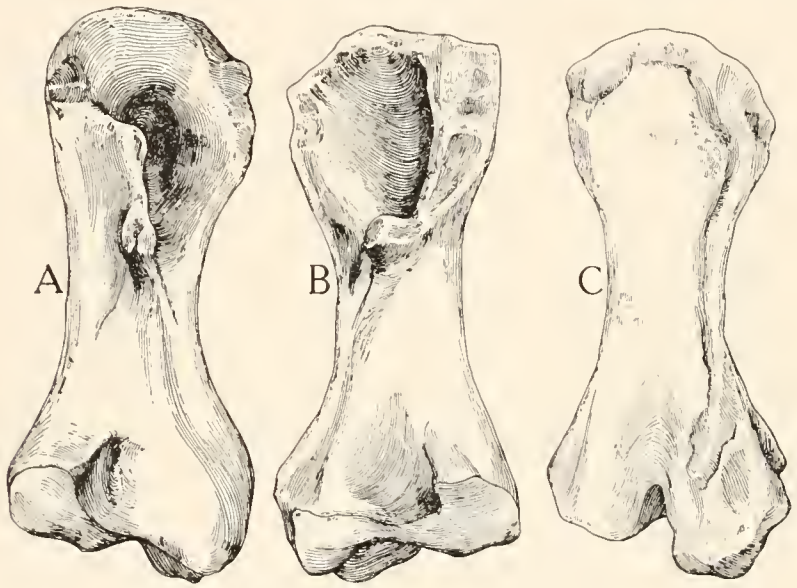

FIG. 14.—*Diasparactus zenos* Case, × ½. A, posterior view of right femur; B, posterior view of left femur; C, anterior view of left femur.

edges turn down sharply and meet in a median symphysis, which finds expression on the lower surface in a sharp keel, continuous with that formed by the pubes. With the exception of the prepubic faces, never seen by us before but described by Broili in a specimen of *Diadectes* from Texas, now in Munich, the whole pelvis differs very little from those of the specimens of *Diadectes* already known and closely resembles that of *Limnoscelis* and *Seymouria*.

We are unable to explain the meaning of the peculiar shelf on the outer side of the crest of the ilium. In *Diadectes* the upper ends of the neural spines, in the dorsal region, are broad and rugose and, in some cases, even expanded; this has led Case to make the suggestion that there might have been an imperfect dorsal armor, such as occurs in *Parciasaurus*, and that the shelf may have been the place of contact with the lower end of a broader plate, or plates, covering the pelvic region. No trace of any dorsal armor has been discovered in any specimen of the family. In *Diasparactus* the dorsal spines, as described below, are higher than in any other known genus of the family and there is no distal expansion or rugosity of the spines; the shelf is fully as well developed, however, as in the genus *Diadectes*.

The *femur* is very similar to that of *D. phaseolinus*, but rather more slender. The head is convex dorsally, but with a deep trochanteric cavity on the ventral face. The articular face is crescentic, confined to the end of the bone and somewhat wider at the inner end. On the outer side of the proximal end is a strong process inclined inward, on the bone of the right side, but this is probably due to crushing and the process normally stood directly out from the body of the bone as in *Diadectes*. The most prominent part of this process is just above the middle of the shaft, and a short ridge extends downward to the middle of the ventral face of the shaft; this ridge can be traced as a low prominence obliquely across the face of the shaft to the outer angle of the lower end. The shaft is proportionately longer than in *D. phaseolinus*, and oval in section, but the outline is marked by the prominence just described and the narrower radial border The lower end has the form common in the pelycosaurs and cotylosaurs; on the inner side is a semicircular face for the tibia and on the outer a more elongate face (antero-posteriorly) for the

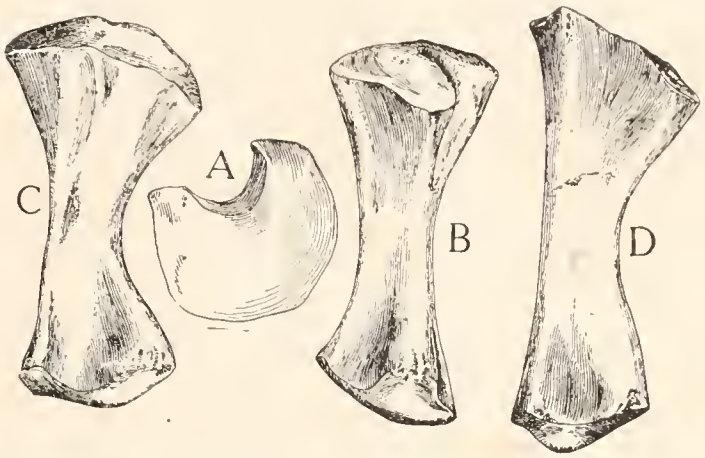

FIG. 15.—*Diasparactus zenos* Case, × ½. A, upper surface of right tibia; B, anterior view of right tibia; C, inner view of right tibia; D, inner view of right fibula.

fibula. The face for the tibia is semicircular in outline and is inclined downward and backward; it is nearly cut off from the fibular face by deep grooves on both the anterior and posterior sides of the bone. Just above the fibular face is a deep pit on the outer side.

In a specimen of *D. phaseolinus*, No. 4684 American Museum, the articular faces of the distal end of the femur are concave with raised edges, indicating the presence of a considerable mass of cartilage; this condition, however, seems to be peculiar to the particular specimen, and as it occurs on many of the articular surfaces may be due to exceptional conditions of fossilization or to the age of the animal —especially as a similar condition does not occur in other specimens identified as belonging to the same species. In *Diasparactus* the articular faces are well rounded and better formed, resembling the condition found in the Pelycosaurs and indicating a more perfect joint. Compared with the femur associated with the type skull of *Chilonyx*, the femur of *Diasparactus* is less rugose, shorter, and the fibular face does not descend so far below the rest of the distal end of the bone. The suggestions of similarity between *Chilonyx* and *Diasparactus* indicated by the position of the quadrates is not borne out by the femora.

The *tibia* is short and heavy, but this is not carried to the extreme seen in *Diadectes* or *Diadectoides*. The proximal face is crescentic, due to the deep incision

on the anterior face of the upper end. The outer half of the face is longer and broader than the inner, which extends rather farther forward and is inclined downward, forward, and slightly inward. The two halves of the face are much more unequal than in *Diadectes*. The heavy proximal end contracts rapidly to a relatively slender shaft, triangular in section. The distal end is expanded anteroposteriorly, but is little wider than the shaft. The face is semilunar, due to a shallow concavity on the inner side of the distal portion of the shaft. The articular surface is convex, presenting a posterior portion which looks almost directly downward and an anterior, inclined upwardly and inwardly; these two portions are not divided into separate faces.

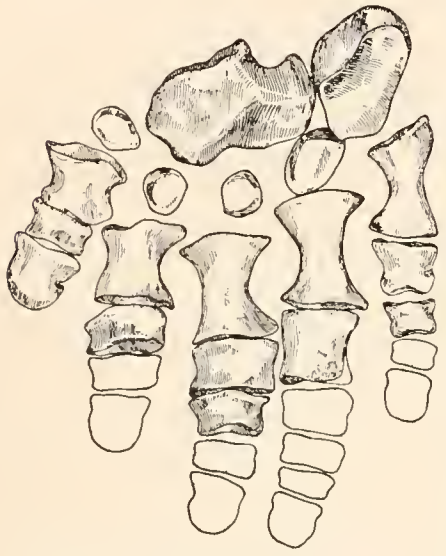

FIG. 16.—*Diasparactus zenos* Case, × ½. Upper surface of left hind foot.

The *fibula* is decidedly different in form from the same bone in *D. phaseolinus*. In that animal the upper end of the bone is nearly circular in outline, joining the shaft below with a sharp change in outline. The lower part of the bone widens gradually and the distal articular surface is nearly flat (see fig. 30, p. 82, Publication 145, Carn. Inst. Washington). In *Diasparactus* the head is formed by a gradual widening of the shaft and is very little thickened. The outer edge of the whole bone is straight, nearly to the distal end, where it turns slightly outward; the inner border is quite concave, the curve becoming sharper toward the distal end. The distal end is considerably wider than the proximal. There are two articular faces; one larger, nearly horizontal, occupying nearly the whole of the distal surface, and a smaller, inner one, inclined upward and inward. The whole bone is very thin, with slight concavities on the inner face just proximal to the edges.

The *tarsus* of the left side is nearly complete and there is very little disturbance; that of the right is less perfectly preserved. On the right side the tibiale and fibulare and two bones of the distal row are in connection, but the tibiale is badly injured. The tarsus, like the carpus, must have contained a considerable amount of cartilage, for tarsalia I, II, III are mere nodules, while the proximal ends of the metatarsals are broad and heavy. The *tibiale* is much nearer in form to that of *Labidosaurus* and the pelycosaurs than to that of *Limnoscelis*. Williston describes the tibiale of *Limnoscelis* as a nearly cuboid bone which in his figure occupies only the inner half of the distal articular face of the tibia. He regarded it as either a tibiale or a tibiale+intermedium, but is inclined to believe that only two bones may appear in the tarsus of the reptiles. In *Diasparactus* the tibiale is rather elongate and, assuming the position in which the bone was found to be correct, is roughly right-angled when seen from in front. The inner face (fig. 17 A, *a*), which was in contact with the fibulare as the bones lay, is wide and triangular in outline; on the lower face of the horizontal portion there is a deep groove, wider and deeper above and becoming shallower toward the lower edge. On the lower part of the inner face there is another groove (fig. 17 A, *b*). The lower end has a large, nearly square face, looking straight downward. The upper part of the horizontal portion carries no articular face, but on the outer vertical edge there are two rough faces, probably articular. The larger looks outward, upward,

and slightly forward; the posterior, smaller face looks directly outward. If the bone is viewed from the inner side its outline is quite suggestive of the tibiale of the Cotylosauria, but it seems that this is more of a coincidence than otherwise and that the true position of the bone is different from that in the order mentioned and that the faces articulate in a different manner. Allowing the bone to remain in the horizontal position in which it was found, which seems quite correct, it lies nearly across the tarsus, its inner end taking a small part in the articulation with the fibula and its large, outer, oblique face accommodating the tibia.

The *fibulare* is oval, with a broad face on the upper side for the fibula and a narrower one on the inner side for the tibiale. The lower and outer edges are thinner, but still quite broad. The distal row consists of four bones. Tarsalia I, II, III are small, oval, flattened nodules with no articular surfaces and indicate the presence of a considerable mass of cartilage in the foot. Tarsale IV is larger, roughly triangular, with broad edges and a deep concavity on the lower surface. There are no traces of centrale bones. The attitude of the tarsus in this and related forms was far different from that in the Pelycosauria or in the modern Lacertilia; the foot was not set obliquely to the axis of the foreleg, but was continued directly forward.

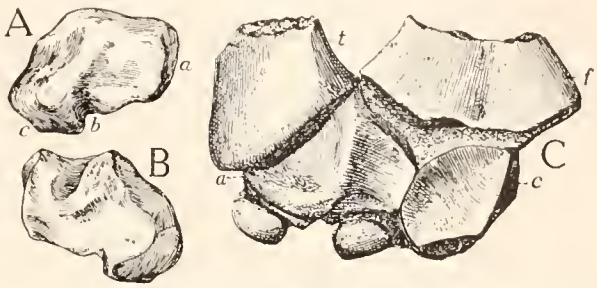

FIG. 17.—A, *Diasparactus zenos* Case, left tibiale from the front, × ½; B, left tibiale of same from the rear, × ½; C, carpus of an unidentified species of *Diadectes*, in the collection of the University of Chicago; *t*, tibia; *f*, fibula; *a*, astragalus (tibiale); *c*, calcaneum (fibulare).

The *phalanges* are similar to those described from the front foot. The metatarsal of the first digit is short and very wide, that of the fourth digit is longer than any in the front foot, and the whole digit was also, apparently, longer. The first phalange of this digit is short, but much wider and heavier than the metatarsal.

The *vertebral column:* The condition of the vertebral column has been described in the general account of the specimen. The *atlas* is wanting; in only one specimen of the Diadectidæ (No. 1075 Univ. Chicago), the nearest related group, has this bone been observed. It is a flat disk, perforated by the notochordal canal, with detached neural arches. The arches were weak, with small and weak posterior zygapophyses for attachment with the axis. It is not known whether they were divided, as in the Stegocephalia (young stages of *Eryops* and *Trimerorhachis*), but in all probability they were. The atlantal intercentrum is preserved in the specimen of *Diasparactus;* it is thick and heavy, with the anterior articular face for the occipital condyle wider than that for the axis.

The *axis:* This is not in connection with the rest of the vertebral column or the skull, but is identified by the neural spine; this is thin and elongated anteroposteriorly, with the posterior edge nearly straight and the anterior edge slanting downward and forward to project over the atlas, quite as in *Dimetrodon* and *Diadectes*. The sides of the neural arches are not expanded and convex as in the dorsal vertebræ. There is a short transverse process for the attachment of a well-formed rib. The centrum is small, with nearly circular faces; the sides are smooth, somewhat contracted, and meeting in a sharp median keel below. The lower edge of the anterior face is beveled by an articular face for the axial intercentrum, which is nearly as large as the first intercentrum.

The *third vertebra* * has lost the neural spine, but judging from the base the spine was broadly diamond-shaped in section with the anterior and posterior edges somewhat extended as in the succeeding vertebræ of the presacral series. The neural arch is slightly convex, beginning to assume the form of the neural arch in all the Cotylosauria, but is still much narrower than those of the dorsal series. The anterior zygapophyses are injured, but were evidently of good size. The neural canal is, as the specimen is prepared, of relatively enormous size, having a diameter greater than that of the centrum; this is apparently natural, but if so is a most surprising feature. The sides and the bottom of the centrum are concealed by the matrix, but it is apparent that the centrum retains the small size seen in the axis and that there was a large intercentrum. It is a notable fact that throughout the presacral series the accommodation for the intercentrum is largely made by the beveling of the anterior face of each centrum and that there is a much smaller face on the posterior end. The transverse process starts from the side of the anterior zygapophysis near the anterior end and runs downward and forward nearly or quite to the anterior face of the centrum at the lower edge; this is somewhat obscured in the third vertebra, but is very apparent in those immediately following. The upper end of the transverse process stands well out beyond a line connecting the outer edges of the anterior and posterior zygapophyses; in this and the rest of the cervicals the characteristic shortening of the transverse process does not appear; it begins at the first of the dorsal vertebræ.

FIG. 18. Upper view of third, fourth, fifth, and sixth cervical vertebræ of *Diasparactus zenos*, × ½.

The *fourth to the seventh vertebræ* have lost the neural spines, but the bases show that they were all rather slender, with the diamond-shaped section described above. The neural arches become gradually wider and rounder until on the seventh they have assumed fully the form characteristic of the order. The centra of the sixth and seventh are rather more elongate than the anterior ones, somewhat narrowed on the bottom line, but without a distinct keel. The intercentrum between the sixth and the seventh is narrow and shallow, not rising much above the lower edge of the centrum; this is the form observed in all of the succeeding portion of the column except the immediate presacrals. The transverse processes are still prominent, but decreasingly so, and in each vertebra they originate a little farther back until in the seventh the upper end rises from a point a little anterior to the middle of the neural arch. The articular face for the rib is flat and runs downward and forward, touching the anterior edge of the centrum near the bottom line, so that if the vertebra is viewed from the lower surface the anterior end is considerably wider than the posterior.

There is a break following the seventh vertebra, but as the next vertebra is of the correct size and form, and especially as the vertebræ were in position as they lay in the ground, it may safely be assumed that the next in series is the eighth and that the lack of a fit is due to the loss of some small amount of matrix, either in the collection or preparation of the specimen. From the eighth dorsal to the twenty-third caudal, the forty-seventh of the complete series, the contact is preserved or, in the caudal series, recorded from the matrix in cleaning.

The *eighth vertebra* is imperfect, having lost the spine and a part of the left side. The neural arch is low and convex, with considerable breadth across the zyga-

* Williston believes that this may be the fourth or fifth. Case believes, from comparison with *Diadectes*, that it is the third.

pophyses, laterally. The outer edge of the upper end of the transverse process is just on a line with the outer edges of the anterior and posterior zygapophyses. The articular face runs down to the anterior edge of the centrum.

The *ninth vertebra* is the first with a complete neural spine; this is oval in section throughout, with the anterior and posterior edges slightly contracted; the upper end is not rugose nor expanded; it terminates in a flat, smooth face.

From the *tenth to the sixteenth vertebra* there is little or no change in form. The maximum width of the neural arches is attained in the tenth and retained to the fifteenth. The upper ends of the transverse processes do not reach beyond the line of the zygapophyses, and beyond the tenth they shorten very rapidly, until in the last of this series they form only very slight prominences on the sides of the centra. The neural spine of the tenth is similar to that of the ninth, but does not exhibit a slight anterior curvature visible in the anterior one; this curvature may be due to accidents in fossilization or may be the last remnant of a

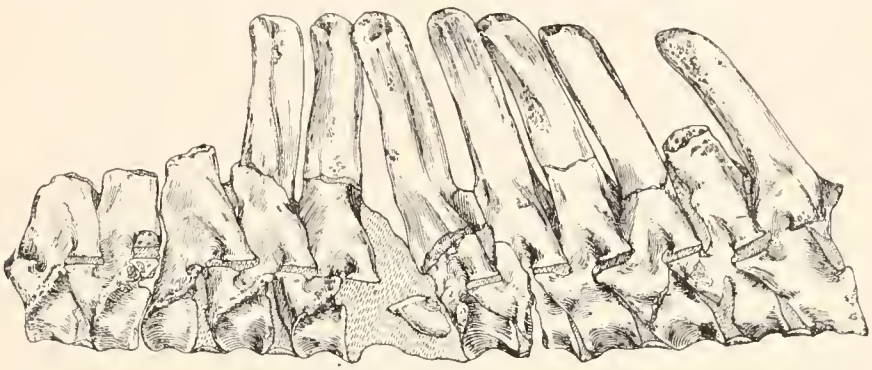

FIG. 19.—*Diasparactus zenos* Case. Lateral view of the last eleven presacral vertebræ, × ½.

decided forward curvature of the spines in the cervical region. On the posterior face of the thirteenth the broken surface shows the edges of distinct hyposphene and hypantrum articulations. The posterior edges of the neural arches of the last vertebra in this series are nearly straight vertically; they descend almost directly from the base of the neural spines and do not overlap the anterior portion of the succeeding vertebræ, as in *Diadectes*. The centra are short, without keels on the mid-line, but are somewhat narrowed below.

The *seventeenth vertebra* is slightly displaced from the sixteenth, but is held in place by matrix. It shows a very decided change in form from the preceding one. The neural spine is a little higher and the neural arch narrower, with steeply sloping sides. The transverse process is here and in the succeeding vertebræ identical in form and condition with those of the type specimen of *Diasparactus zenos*, No. 4794 Am. Mus. Nat. Hist. Cope Coll. The portion of the original description applicable is here repeated.*

"This new genus and species of the family Diadectidæ is characterized by the small size of the centra compared to the height and spread of the neural arches, and the short transverse processes. The whole vertebra is relatively very thin antero-posteriorly, so that while it has the general form of all members of the family, it looks much higher and wider and the small centrum gives it something of a high-shouldered kite-shape, when viewed from the front or rear. The transverse processes are exceedingly short, never extending out beyond the edges of the zygapophyses and in most cases not reaching so far."

* Case, Bull. Am. Mus. Nat. Hist. vol. XVII, p. 174, 1910.

The remaining presacrals are similar in form. The neural spines become a little heavier and shorter, the neural arches are narrower, the transverse processes become shorter by reduction of the lower end, not reaching to the anterior end of the centrum, and the position of the neural arches changes so that the posterior zygapophyses hardly reach beyond the posterior edge of the centrum, while the anterior ones reach far forward, almost to the middle of the preceding centrum. In the dorsal series the condition is almost exactly the reverse of this last-mentioned point. Between the last two presacral vertebræ the intercentra are very broad antero-posteriorly, but still quite shallow.

The *sacral vertebræ* are two in number; both have lost the neural spines. The first has a very short and narrow neural arch with well-developed anterior but weak posterior zygapophyses. The sacral rib of the first is very heavy; its proximal attachment is from the anterior end of the anterior zygapophysis to beyond the middle of the neural arch. The body of the rib extends nearly straight downward, but has a slight posterior inclination. The lower end is concealed in large part by the ilium, but it can be seen that it is a broad, thin plate with a wide posterior extension, which was applied to the inner side of the crest of the ilium. The whole vertebra is set rather high, so that the crest of the ilium does not rise greatly above the middle of the neural arch.

The *second sacral vertebra* resembles the first in most regards, but the ribs are very much smaller and more slender. Starting with a strong attachment to the sides of the neural arch and the centra, they rapidly dwindle to a very slender process without any distal expansion. The lower part extends downward and then turns backward, just touching the inner side of the ilium. These ribs take very little part in the support of the pelvis and resemble the ribs of the anterior caudal vertebræ very closely. It might be said that there is but a single sacral vertebra, so small is the share of the second sacral vertebra in the support of the ilium. The sides and bottoms of the two vertebræ are hidden by matrix, but as they are slightly separated in the specimen it may be said with certainty that they were not closely united in life.

The *anterior caudal vertebra* closely resembles the second sacral. The spine is the only one of the caudal series which is preserved. It is short and sharply curved to the rear, so that the flat distal end looks directly to the rear. The ribs have strong triangular heads firmly attached to the centra and occupying most of the side; they are rather elongate and, like the rib of the second sacral, extend downward and outward, but turn sharply to the rear at the distal end. The lower face of the centrum is wide, slightly concave antero-posteriorly, and gently convex from side to side. There is no trace of a keel.

The *second to the sixth caudals* have the same form as the first, becoming gradually smaller. The ribs maintain the same form, but rapidly shorten. The lower surface of the first five is concealed by matrix; the sixth and seventh are poorly preserved and as yet not freed from the matrix. It is uncertain at what point the chevrons began.

The *eighth caudal* has a relatively small neural arch set well forward on the centrum. The spine was slender and inclined slightly forward, but, in common with all the caudals, except the first, has been destroyed. The base of the centrum is shortened by the development of a large face on the anterior end for the accommodation of the head of a chevron bone. The posterior end is beveled by a similar but smaller face. Between the eighth and the ninth centra is the base of a badly injured chevron; this is the only one of the series of chevrons that has been preserved and it is so badly injured that little more than its presence can be noted.

From this point back the character of the vertebræ changes regularly and very slightly. The last trace of a rib is seen on the eleventh or twelfth. The sixteenth and seventeenth still have well-formed neural arches located on the anterior half of the centrum; the posterior zygapophyses are elongated. From this point back to the twenty-third, the last preserved, the neural spines are low, almost rudimentary, and the zygapophyses are elongated, interlocking strongly at first, but becoming reduced in the posterior part of the tail. In only the last few vertebra is there any tendency for the centra of the vertebræ to become at all elongate, and even here it is very slight. There is no indication of any great length of tail.

The *ribs:* Anterior to the first vertebra in series, reckoned as the third cervical, there is a well-developed rib, of moderate length, lying in the matrix just within the edge of the scapula. This is the rib of the axis; it has a wide, undivided head and a slender shaft terminating in a point. The ribs of the third, fourth, and fifth vertebræ are in general form similar to the ribs of the same vertebræ in *D. phaseolinus*, but as they are injured on the left side and covered by the scapula on the right, the exact form can not be given. The rib of the third vertebra (fig. 21 A) has an elongate, undivided proximal end; beyond this it contracts to a narrow shaft; the anterior edge is straight to the distal end, but the posterior is extended backward in a sharp point almost at right angles to shaft for a centimeter or more and then obliquely forward to the distal end; this gives a narrow, triangular form to the rib, resembling the same rib in *D. phaseolinus*, but longer. The shape of the next two ribs is less certain, but they are larger than the third and were evidently of the same triangular form. The fifth is the largest of the series. The sixth rib is normal in form, with an undivided head. There is no trace of the plates which overlie the sixth, seventh, and eighth ribs in *Diadectes*. Beyond the sixth the ribs are not preserved in place until the fifteenth and sixteenth are reached. On the left side of the series from the eighth to the fifteenth are attached the imperfect shafts of five ribs, but neither the proximal nor the distal ends are preserved. The shafts, as preserved, are rather more slender than in *D. phaseolinus*. On the left side of the fifteenth (fig. 21 B) and sixteenth the ribs are retained in place, but are bent back parallel to the column. The heads are rather short and are undivided; the shaft of the rib stood almost directly out from the vertebræ, with little downward curvature.

FIG. 20.—*Diasparactus zenos* Case. Lateral view of the ninth to the twenty-third caudal vertebræ, × ⅓.

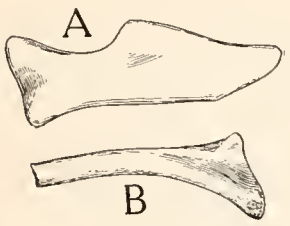

FIG. 21.—*Diasparactus zenos* Case, × ½. A, rib of third cervical vertebra from left side; B, head of rib attached to right side of fifteenth vertebra.

There is no trace of any *abdominal ribs.*

THE RESTORATION OF DIASPARACTUS ZENOS.

In the restoration presented (fig. 22) we believe that there is very little that can be questioned. The skull, though badly shattered, presented nearly all the characters, and its resemblance to both *Diadectes* and *Animasaurus* is so close that we feel justified in all the points which we have recorded. Neural spines are present both in sufficient number and in sufficiently diverse positions to render certain their general characters throughout the column. The atlas is restored *in toto* from *Diadectes*, but the presence of the atlantal and axial intercentra gives

an idea of the character of the lower surface, and the similarity of the axis to *Diadectes* renders it very probable that the atlas was of the form shown. Ten vertebræ have been added to the extremity of the tail; this may be wrong by one or two either way, but scarcely more. Williston thinks the tail to have been rather longer than does Case. That chevrons were present is shown by the base of one, and the form of these bones varies so little, in a general way, that it is safe to conclude that they were nearly as represented; they may have been a little longer and may have had a slightly different inclination. The phalangeal formula was very certainly the usual one, 2, 3, 4, 5, 3–4; this is shown by the presence of digits on one or another foot carrying 2, 3, 4, and 5 phalanges. We have assumed that the position of the tarsus, as it lay in the ground, was correct and little if any disturbed; it seems very satisfactory as compared with other forms. The presence of two centrale in the tarsus is not certain and is improbable. For all other points there is full evidence from the skeleton.

That *Diasparactus* was a member of the family Diadectidæ there can be no doubt. The general form of the body is strikingly similar and the individual

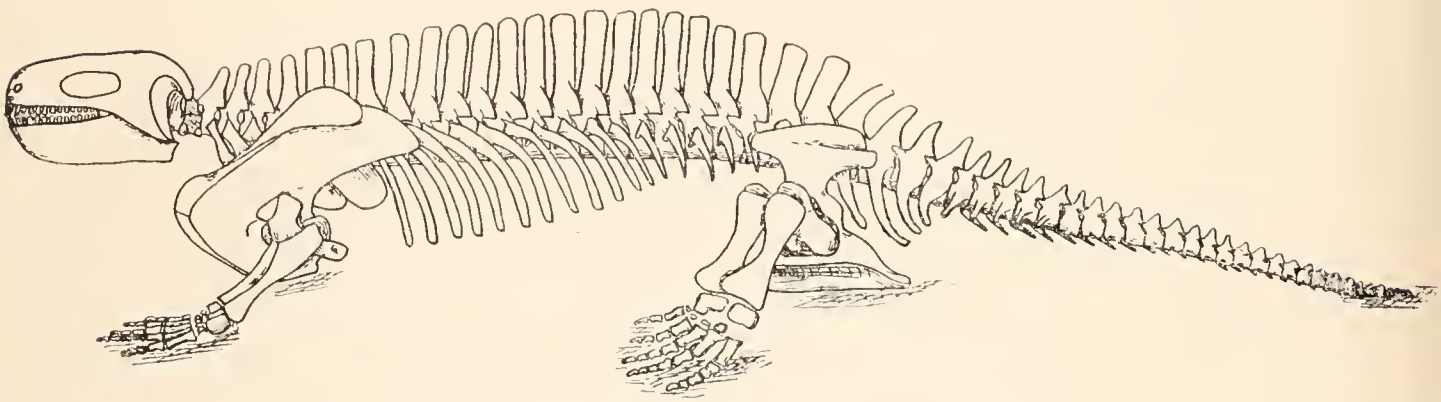

FIG. 22.—Restoration of *Diasparactus zenos*. About $\frac{1}{8}$ natural size.

bones show differences that can not be reckoned greater than generic. The skull is closer to that of *Animasaurus* than *Diadectes*, but possesses characters of both. The development of the three broad ribs in the cervical region is another close resemblance to *Diadectes*, which we doubt not will be found in *Animasaurus* when the skeleton of that genus is discovered. The absence of the plates over the sixth, seventh, and eighth ribs may be natural or may be due to accident. The presence of a well-developed rib on the axis is a new but not unexpected feature. The shoulder and pelvic girdles and the limbs are strikingly similar to those of *Diadectes;* the most apparent differences are in the vertebræ. The high and more slender neural spines are distinctly indicative of habits somewhat different from those of *Diadectes;* if the idea be retained that the Diadectidæ were in process of developing a dorsal armor similar to that of *Parciasaurus*, which was perhaps realized to some extent in *Diadectes*, then *Diasparactus* may be regarded as representing an early stage in the process.

The animal had gone far toward attaining the strongly articulated vertebral column forming the axis of what must have been a very stiff and rigid body, so evident in the members of the family, but had perhaps not yet abandoned freedom of motion in the dorsal series so extensively as had *Diadectes;* this is perhaps borne out by the less powerful sacrum; in *Diadectes* the two vertebræ support the pelvis,

in *Diasparactus* the second plays little part, as indicated above. For the reasons cited in the description of the foot, we are of the opinion that the Diadectidæ were not aquatic animals, but marsh-dwellers; we believe these animals to have been very sluggish, harmless eaters of vegetation or small invertebrates, and to have been able to present no more than a passive defense against the attacks of the larger carnivorous forms, pelycosaurs, or forms yet unknown. Such habits would inevitably lead to concealment and to the persistence of any forms favored by the development of some form of protection, as an armor. We know that the period in which these animals lived was one of those, frequently repeated in the history of the world, in which there was a keen contest between attack and defense, the development of a peculiarly efficient type of predatory form (in this case the pelycosaurs of the genus *Dimetrodon*) was paralleled by the development of armor on the weaker forms (in this case both amphibians and reptiles). It is very probable that *Diadectes* followed the general trend. The lateral position of the orbits does not indicate habits such as those of the Stegocephalia, in which the orbits are near the surface of the skull and look largely upward. It is possible, but only offered as a suggestion, that the large size of the orbit may indicate a large eye and so nocturnal or crepuscular habits.

Measurements.

	M.
Total length of the animal, as restored	1.35
Length of 10 vertebræ added to complete the tail	.105
Length of skull, as restored	.167
Width of skull, across quadrates, as restored	.154
Length of arc of slightly flattened right clavicle	.159
Length of arc of right scapula	.180
Width of anterior end of same	.128
Extreme length right humerus	.151
Width proximal end of same	.084
Width distal end of same, slightly distorted	.094
Width distal end left humerus	.081
Length right ulna	.118
Length right radius	.084
Length complete third digit of manus, left side	.073
Length metacarpal of same digit	.026
Width proximal end of same	.024
Height of ninth vertebra	.117
Breadth across posterior zygapophyses of same	.074
Length across anterior-posterior zygapophyses, same	.039
Length bottom line of centrum, same	0.023
Height of fifteenth vertebra	.134
Breadth across posterior zygapophyses of same	.084
Length across anterior-posterior zygapophyses of same	.038
Length of bottom line of centrum of same	.029
Length of bottom line of pelvis	.166
Height of pelvis to top of ilium, a little exaggerated by pressure	.016
Length of crest of right ilium	.116
Breadth across center of acetabulum	.092
Length of right femur	.146
Length of right tibia	.102
Length of right fibula	.118
Approximate breadth of tarsus	.082
Length of fourth digit of pes, right side, minus terminal phalange	.086
Length of metatarsal of same	.037
Length of first digit of pes, left side	.045
Breadth of proximal end of metatarsal of same	.023

CHAPTER V.

DESCRIPTION OF A NEARLY COMPLETE SKELETON OF OPHIACODON MARSH.

By S. W. Williston and E. C. Case.

The genus *Ophiacodon* was proposed in 1878 by the late Professor Marsh, to include two new species of reptiles based upon fragmentary and disconnected material collected by the late David A. Baldwin from a bone-bed near Poleo Creek in Rio Arriba County, New Mexico. No distinctive characters were given for the genus, nor was it possible to give such, since the two species Professor Marsh described, *O. mirus* and *O. grandis*, represent not only two distinct genera, but two different orders and classes as well; the second species belongs to the temnospondylous genus *Eryops*, or an allied form. The characters given in the brief description of the genotype were so meager that it was impossible to identify the form without comparison of the type. The genus therefore remained doubtful till recently, when Williston examined the type specimens in the collections of Yale University. The genotype, *O. mirus*, was described by Marsh as follows:

"A third genus of reptiles allied to the last described [*Sphenacodon*] is indicated by various well-preserved remains from the same locality. The teeth are all carnivorous in type, conical in form and all are similar. Those in the anterior part of the jaws are recurved, and in general shape resemble those of serpents. The rami of the lower jaws are united by cartilage. The vertebræ are very deeply biconcave, and even perforate, and the intercentral bones are large. In the present species the teeth are nearly smooth, and somewhat compressed.

"The following measurements indicate the size of the reptile:

"Extent of anterior sixteen teeth in dentary	75 mm.
Extent of five lower teeth	20
Height of crown of fourth lower tooth	10
Depth of lower jaw at symphysis	15
Extent of seven anterior maxillary teeth	33
Height of crown of first maxillary tooth	9
Antero-posterior diameter of crown	3"

Of the original material, only the fragmentary mandible and maxilla could be positively referred to this genus and species. A study of the associated material in the type collections, by a process of elimination, indicated various other parts of the skeleton which might, provisionally, be associated with the genotype. The greater part of this material came from a bone-bed, hereinafter designated as the Baldwin Bone-bed, in which the bones were widely distributed, and almost wholly disconnected. Descriptions and figures of such bones of this bone-bed as seemed to be conspecific were given by Williston in his American Permian Vertebrates, p. 81, plates XXXIV–XXXVII. A comparison of these figures with those of the present paper will show that most of the bones there provisionally referred to *O. mirus* were correctly identified, as follows: clavicle, scapula, humerus, radius, ulna, ilium, femur, and tibia. The vertebra figured and described is more doubtful, since it differs materially in its more elongated spine. The sacrum, very doubtfully referred to this genus, belongs with *Sphenacodon*.

The material herein described, consisting mostly of a single skeleton (Catalogue No. 650 University of Chicago) of remarkable completeness, came from another bone-bed, which for convenience is called the Miller Bone-bed, after its discoverer, Mr. Paul C. Miller. This bone-bed is about half a mile east of the Baldwin Bone-bed, and apparently in quite the same horizon. The skeleton, as fossilized, must have been nearly or quite perfect. Perhaps a half or more of the tail, the distal half, had been weathered out of the matrix and strewn on the surface below. Unfortunately, before the skeleton, which lay about a foot above the chief bone-layer, was recognized a stroke of the pick had mutilated the sacral region, which, with some of the adjacent spines and the underlying left foot, was lost in the loose material thrown over the dump. Although diligent search for these lost parts was later made, not many of them were recovered. Dr. Williston has, regretfully, to add that he alone is responsible for the mutilation.

Upon the recognition of the skeleton lying in an orderly position, the specimen was carefully traced out and removed by Mr. Miller, with our aid, in a single large block of matrix secured by bandages. The skeleton, as received in the laboratory, was carefully cleaned of its investing matrix on the upper (right) side, and then embedded in a plaster mold, after which it was turned over and worked out from its better preserved lower (or left) side. As it lay in the matrix (pl. 1, fig. 2) it had what seemed to be a most remarkably natural position, with its various parts all in articulation, or nearly so, as far as the pelvis. The right foot and hand, falling on their inner sides, had their inner digits partly folded under the others, but with little disturbance of their articulations. The shoulder-blade of the upper side had slipped downward and forward a few inches. Apparently after death, and before maceration had gone far, the cadaver had been gently pushed cephalad and ventrad some 6 or 8 inches, dragging the under limbs dorsad and caudad, bringing the left hand under the lumbar vertebræ and the left foot under the pelvis. The curve of the dorsal vertebræ, as the skeleton lay, is perhaps a trifle greater than was usual in life, and the skull evidently had suffered more flexion than was commonly assumed in the living animal. These positions and curves, however, have not been greatly modified in the mounted skeleton (pl. 1, fig. 3), the skull and vertebræ, for the most part, being still united by their original matrix.

Lying on the same level, and perhaps 2 or 3 feet distant from this skeleton, there was another (No. 652) skeleton of the same species, almost identical in size and characters, the larger part of which had been washed out from its matrix and strewn down the hillside, intermingled with the distal caudal vertebræ of the more complete skeleton. From the matrix of this second specimen the pelvis, posterior, dorsal, and sacral vertebræ, the nearly complete left hind leg and a part of the right one, and various other bones were recovered, parts which, fortunately, supplement the more complete specimen almost perfectly. Furthermore, *Ophiacodon mirus* seems to be well represented in the underlying bone layer by isolated bones, many of which were collected, but have not yet been worked out. The skeleton, therefore, as herein described, lacks some distal caudal vertebræ and the vertebral spines of the posterior dorsal and sacral regions only. From all of which it results that, aside from the intimate structure of the skull, there is perhaps no genus of Permian vertebrates now more completely known than *Ophiacodon*, unless it be *Limnoscelis*.

The matrix of the Miller Bone-bed is a dark brown, indurated sandy clay, weathering loose near the surface, but very hard, almost stony, farther in. It was removed rather easily from the bones, leaving the original smooth surface.

The *skull* of *Ophiacodon* * is remarkable among Permian vertebrates for its relatively large size and delicacy of structure. In part the result, perhaps, of the extreme thinness of most of its bones, the skull was more or less compressed from side to side in fossilization, though without affecting its general shape and contours. So frail is its structure that it was found inexpedient to remove it entirely from its supporting matrix. It was, therefore, carefully cleaned of its investing matrix on its upper or right side and embedded in a plaster mold, after which it was turned over, with the rest of the skeleton, and cleaned on the other, the better-preserved side. Both sides have been photographed and studied by us, but the right side is no longer accessible, embedded as it is in plaster for the better preservation of the specimen.

The skull is remarkably narrow, high, and long. The very small nares are at the extreme front end; the small orbits are far posterior. The upper side is flattened in the frontal and parietal region; its greatest width is just back of the orbits. The occipital region forms a declivity, as in *Dimetrodon*. The parietal foramen has not been detected with certainty; it must have been small. Immediately in front

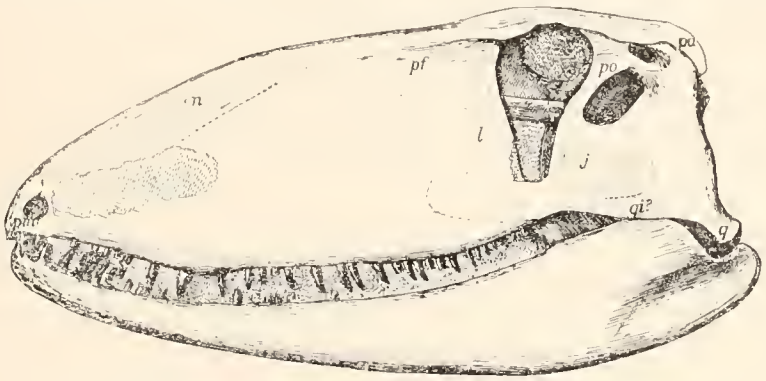

FIG. 23.—*Ophiacodon mirus* Marsh. Lateral view of skull, × ⅓. *pa*, parietal; *po*, postorbital; *pf*, prefrontal; *l*, lachrymal; *j*, jugal; *qj*, quadrato-jugal; *q*, quadrate.

of the orbits the upper surface narrows; thence to the nares the border, formed chiefly by the nasals, is gently convex in outline. Doubtless in life the very broad sides of the face were gently convex, but, as preserved, the thin bones forming them are nearly in contact, producing a light concavity between the thickened alveolar border of the maxilla and the thickened nasal border; the bones of this region are scarcely thicker than writing paper, for the most part, and are so cracked as to render impossible the certain determination of their connecting sutures.

In fig. 23 the skull is shown as it lies in its matrix, except that the two posterior premaxillary teeth have been brought into anatomical association with the first one. The general shape of the skull, as shown, seems to be quite that of life; possibly the dentigerous margin of the maxilla is a trifle too convex in outline. The nares, as has been said, are very small, and are situated near the extreme front end of the skull. The orifice of each naris is nearly circular in outline, directed laterally and perhaps a little forward in life. The orbits also are remarkably small in comparison with the size of the skull. They are subtriangular in shape, broader above, the lower end separated from the posterior end of the maxillæ by the mod-

* Ophiacodon mirus Marsh, American Journal of Science, xv, 411, May 1878; Baur and Case, Trans. Amer. Phil. Soc., n.s., 1899, p. 5, 1907; Williston, American Permian Vertebrates, p. 81, plates XXXIV–XXXVII, Oct. 1911.

erately broad jugals. Above, the orbits are roofed over by a projecting plate from the frontals. The opening of each orbit, as preserved, looks laterally and not at all upward, and this must have been essentially the condition in life. The posterior border, formed by the postorbital above and the jugal below, is thickened, as is also the antero-superior border. Below, in front, the margin is very thin, and the precise edge here has been lost in preparation. Immediately back of the upper, dilated, part of the orbit, and separated by a narrow but firm bar, is the relatively small, oval, lateral temporal fenestra, an opening 25 mm. in its greater, 13 mm. in its conjugate diameter, the former at an angle of about 45 degrees with the condylar-narial axis of the skull. Its postero-inferior margin is thin; elsewhere the border is thicker and rounded. Above, this vacuity is separated by a thick, subcylindric or oval bar from a smaller, oval vacuity or foramen, the supratemporal fenestra, which is about 12 mm. in its greater diameter at the bottom of a fossa, which is partially over-roofed by the posterior prolongation of the parietal. There seems to be no doubt that this opening is a normal one, not due to some accidental separation of contiguous bones, since it is alike on the two sides of the skull. On each side the clay matrix filling the fossa and vacuity was removed with care, proving conclusively that the thick, rounded, smooth, and deep margins were everywhere normal, without signs of sutural roughening or fractured surfaces. This opening, bounded below by the thickened supratemporal arcade, which evidently is composed of the united postorbital and squamosal, posteriorly by what is certainly the squamoso-parietal bar, and superiorly by the parietal, can be interpreted as nothing else than a true supratemporal fenestra.

Below and back of these vacuities there is a broad expanse of thin bone, doubtless composed of a squamosal element, the jugal and the quadratojugal. The striations on the clean surface of the bones in this region, as also the position of lines which seem to be sutural, indicate their relative extent and articulations about as they are shown in the figure. With these interpretations, the jugal in front forms only a small part of the free lower border of the maxillo-quadrate arch. A sutural line seems to distinguish the jugal from the post-orbital above, as shown in the figure between the orbit and lateral fenestra. Posteriorly the diverse striation and an intervening sutural line distinguish the jugal from an element that is doubtless the true quadratojugal, which extends far forward on the lower, free border of the arch. The position of this suture is very different from that bounding the jugal behind, positively and definitely known in *Dimetrodon*. In this genus there is but one bone articulating with the jugal posteriorly, the prosquamosal of Case, the squamosal of authors; at least neither of us is convinced of the presence of a lower bone articulating with the jugal, which if present must have joined its extreme tip only, taking no part whatever in the margin of the temporal fenestra.

Case believes that there is no lateral quadratojugal bone in *Dimetrodon*, but that the bone properly so-called is attached to the posterior side of the quadrate, extending upward. A recent examination of the structure of *Dimetrodon* in this region by Williston in material that is, perhaps, as good as any known, tends to convince him of the general correctness of Case's observations, though he is not at all assured of the correctness of his interpretations. The squamoso-jugal suture in *Dimetrodon* passes backward obliquely from above downward to the extreme tip of the jugal. Back of the jugal, covering the quadrate, there is an element which seems to articulate with an upper bone lying posterior to that identified as the prosquamosal by Case. Whether or not this bone touched the extreme tip of the jugal Williston can not decide, but he thinks not. Between it and the quadrate posteriorly there is a distinct foramen, identified as the quadrate foramen by Case.

These relations are proven incontestably by material in the collections of the University of Chicago, and Williston vouches for them. The best evidence we have seen of the presence of a lateral quadratojugal bone in any pelycosaurian reptile is that furnished by the present specimen.

The posterior thickened border of the quadrate slopes obliquely backward from the long axis of the skull. How much of the quadrate is actually visible from without, how much is covered by the roof bones, can not be said. There is certainly no quadrate foramen.

The face in front of the orbits, as has been said, is of great extent. Sutural lines can not be detected, though the longitudinal striation of the broad, long, and somewhat thickened nasals indicates their width, and probably their length, reaching far back toward the orbits. The prefrontal seems to be large, and the extent of the jugal seems to be indicated by striation and sutural lines. Whether the lachrymal (postnarial) extends the whole distance to the margin of the naris, as in the cotylosaurs, is doubtful; certainly if it does it must be a very slender bone.

The *maxilla* is a very long bone, with its dentigerous border somewhat thickened and convex in outline. Twenty-nine maxillary teeth are preserved, with vacant spaces for six or seven more, which, if present in life, must have been lost before fossilization. Possibly the whole number of teeth in this bone may have been 36. The teeth are slender, conical, recurved, and pointed, and they do not vary much in length as far back as the middle of the series. At about the junction of the first and middle thirds of the series there is a distinctly stouter tooth, corresponding to the large maxillary tooth of *Varanosaurus*. The maxilla is thickened above it, and the dentigerous border here is more convex or subangular in outline. The teeth extend posteriorly to opposite the lower angle of the orbit. In the mandible, so far as can be observed, the teeth are all uniformly slender, especially the more anterior ones, with the exception of the first one or two, which seem to be stouter. In the premaxillæ there are three teeth on each side, all larger than the ones immediately following in the maxilla; the foremost is perhaps as stout as the enlarged maxillary tooth.

The *mandible* is long and slender, with a marked concavity of its alveolar border corresponding to the convex dentigerous border of the maxilla. The mandible is a little thickened in front, where the two sides meet in a short symphysis about an inch in length. The coronoid angle is not high; its border is gently convex above, where it slightly underlaps the free border of the quadratojugal. In the space left free back of the teeth, between the jugal and the mandible, the rather broad surface of the pterygoid, or ectopterygoid, is visible; the bone clearly abutted against the mandible in life. As regards the structure of the mandible little can be said, save that the very long splenial meets its mate in a symphysis, as is usual in the early reptiles.

The present specimen seems to demonstrate, for the first time in a Paleozoic reptile, the normal presence of both supratemporal and lateral temporal fenestræ.*

* Neither of us is quite convinced of the presence of both vacuities in the Proganosauria and Proterosauria. The presence of the upper vacuity in *Paleohatteria* has been, we believe, assumed because of the resemblances otherwise of that genus to *Sphenodon*. Credner, in his original description of the genus, alludes very briefly to its presence as "wahrscheinlich"; apparently no certain evidence of its existence was found in any specimens which he studied. In a later paper he restores the skull after *Sphenodon* and says the vacuity is present, but gives no reasons for this statement. We have seen that other Permian reptiles having like "rhynchocephalian" characters do not have two vacuities on each side, and the presence of an upper one in *Paleohatteria* must remain a subject of legitimate doubt until additional evidence incontestably demonstrates its presence. A very recent examination of the type specimens of *Paleohatteria* in Leipsic has convinced Williston that only one temporal vacuity is present.

In *Dimetrodon* Case has asserted the presence of an upper vacuity, but the evidence is now apparently conclusive, and is so accepted by him, that, in some specimens at least, there is no upper vacuity; and Williston, not having studied the matter thoroughly, is not in a position to express a positive opinion as to its normal absence, though he thinks such is the case. It will, perhaps, require additional specimens of *Ophiacodon* to prove its constant occurrence in this genus, but it is our firm opinion that the opening in the present specimen is a normal character of the genus; it certainly is of this specimen. And this is said with a full appreciation of the reputed fenestræ in the skulls of *Procolophon* and *Dicynodon*, later shown to be errors.

As a bit of philosophy we may say that observers are often led into the recognition of characters that accord with preconceived opinions. If one finds many characters agreeing in different forms, he is naturally disposed to assume that other characters do also. For a long while *Procolophon* was supposed to be closely related to the rhynchocephalian reptiles—a supposition now summarily disposed of, we think—to such an extent that it was located with the "Diapsida" and "Diaptosauria" even. But *Sphenodon* and the Rhynchocephalia have been responsible in the past for many taxonomic sins, and we have not yet quite escaped from the shadow of their misleading influence.

In the present reptile the presence of a supratemporal fenestra was wholly unexpected, and its discovery was rather a shock, since it seems almost hopelessly to confuse the taxonomy of the Reptilia. That there is such a fenestra in the present genus is, we think, beyond reasonable doubt. What is its significance? It will be seen that not only the upper vacuity, but the lower one also, is remarkably small, smaller proportionately than is known in any other double-arched reptile. Are they rudimentary? Or vestigial? Is their small size due simply to the remarkable development of the facial part of the skull without a corresponding development of the posterior part? Against this explanation is the fact that the temporal region of *Ophiacodon* is, for the most part, covered by a broad expanse of bone, necessitating the assumption that in the evolution of this particular type of skull from some smaller one having proportionately larger vacuities everything has developed except the vacuities. This hypothesis we think may be rejected. There seems to be but one conclusion—that the openings are rudimentary.

The presence of one or two temporal vacuities has hitherto been regarded as a sort of fetich in reptilian taxonomy and phylogeny—as a crucial test of relationships, not only of ordinal but even of subclass value in classification. For some years past they have been considered as a sort of *noli me tangere* character, in that, whatsoever of iconoclasm is permissible in regard to the feet, limbs, girdles, and vertebræ, hands must be kept off the sacred temporal region of reptiles. But if we do not invade the sanctity here we shall be led into a dangerous morass of speculation. In all other respects *Ophiacodon* is not only a "synapsidan" reptile, but a primitive one at that. To separate the form ordinally and classify it with the "Diapsida" would be taxonomic speculation run wild.

Could we know that *Ophiacodon* is the beginning of a morphological phylum that ended in the Archosauria or Rhynchocephalia we would be quite justified, notwithstanding all of its other and intimate relationships with the one-arched or synapsidan forms, in separating it as the representative of a distinct order of reptiles. In any true phylogenetic classification the lines of descent must be followed back to where they diverge, to where the branches ultimately are separated by nothing more than specific characters, since in the ideal classification of animals and plants the truest is that in which orders, families, and genera are

ultimately distinguished by specific characters only, where the chain from ancestor to descendants nowhere lacks a single link. No character is ever more than varietal until it is fixed and isolated physiologically by heredity and time.

One may be speculative and assume that *Ophiacodon* is really the beginning of the double-arched phylum, the beginning of a subclass, but there is not the slightest proof that such is the case. It will be many years before such an hypothesis can be proven or disproven, if it were ever possible, and classifications based upon hypotheses are unscientific. If the present form is merely a "mutation" or sport, then certainly the presence of a supratemporal vacuity has no taxonomic value, for we have no faith in the theory that species ever arise in such sudden ways. In other words, the most profound taxonomic characters must have had beginnings when they were merely varietal or specific; not till time and long descent have fixed them do they achieve a higher rank. In the present case we are convinced that, without further evidence to the contrary, the presence of two temporal vacuities and two temporal arches in *Ophiacodon* can not be assumed to have more than generic value.

Vertebræ and ribs: As has been stated, the vertebral column as collected was without break or even noticeable disturbance as far back as the sacrum, lying

FIG. 24.—*Ophiacodon mirus* Marsh. Cervical vertebræ from the side, the sixth also from in front, × ½. *ax*, axis; *an*, atlantal neuropophysis; *o*, odontoid; *r*, *r*, ribs; *q*, quadrate; *pa*, proatlas.

with the skull and all or nearly all the ribs in natural articulation. Six or seven of the vertebræ may properly be called cervical, and twenty or twenty-one dorsal; the entire number, as in *Dimetrodon*, *Varanosaurus*, *Theropleura*,* and probably all other pelycosaurs in the narrower sense of the word, is twenty-seven in all certainty.

Proatlas (fig. 24, *pa*). A proatlas has never before been recognized in an American Paleozoic reptile. Its existence in the present genus was not unexpected, since Williston has already suggested that the facets on the sides of the foramen magnum in *Dimetrodon* are for the articulation of this bone.† In the present specimen the proatlas lies quite in position, articulating posteriorly by a well-formed zygapophysis on each side with the arch of the atlas, and in front on each side with a facet on the margin of the foramen magnum. Because of a slight injury on the right side, it can not be said positively that the element is single, though in much

* Twenty-six presacral vertebræ back of the atlas are figured by Case in *Theropleura retroversa* (Publication 55, Carnegie Institution of Washington, pl. XIII, fig. 1).

† American Permian Vertebrates, p. 93.

probability it is. It forms a sort of bridge between the atlas and the occiput, above the spinal canal, with an obtuse protuberance or rudimentary spine above on each side, like that on each atlantal arch.

Atlas (fig. 24): The atlas is preserved perfectly on the left side. Each neurocentrum is slender, curving back to articulate, by a well-formed zygapophysial facet, with the axis at the base of the spine in front. On the front of each arch above there is a zygapophysial facet, slightly constricted from the arch itself, for articulation with the postzygapophysis of the proatlas. Anteriorly a process descends downward and backward, articulating at its extremity with the atlantal rib, which lies closely in position in the specimen. The neurocentrum, as a whole, differs only a little from that figured by Williston in his American Permian Vertebrates, plate XXXIV, figs. 10, 11, from the Baldwin quarry, the chief difference consisting in the more slender process which is represented by a mere protuberance in the atlas of *Ophiacodon*. In much probability the figured neurocentrum belongs with *Sphenacodon*. The arch is supported chiefly by the odontoid, resting only slightly upon the atlantal intercentrum below. The intercentrum is of somewhat larger size than the intercentrum between the odontoid and the axis.

The atlas, it is seen, is of a primitive type, almost identical in structure with such vertebræ as are known in the tails of certain temnospondyls, with the omission of the chevron. In fact, the union of the neurocentra with each other and with the intercentrum would result in an almost typical embolomerous vertebra.

This condition of the atlas in these primitive reptiles suggests certain conclusions. The reptilian atlas could not possibly have been evolved from the atlas of any known amphibian. In the temnospondyls the atlas is composed exclusively of the paired neurocentra fused with the intercentrum; the pleurocentra have, apparently, disappeared entirely. The proatlas also is quite unknown in any amphibian. The proatlas is generally regarded as the remnant of a preatlantal vertebra which has disappeared in the reptiles, and the presence of zygapophysial articulations in these early reptiles would substantiate that theory. Gadow, however (Evolution of Vertebral Column, etc.), insists that the proatlas is merely the spine of the atlas. It has been known for some time that the amphibian occiput, whether of living or ancient forms, does not correspond to the reptilian; and we also know that the atlas in the two classes is not homologous. If, then, the corroborative proof furnished by these reptiles supports the theory that the reptilian atlas is in reality at least the second, perhaps the third vertebra of the amphibians, it would seem probable that the amniote atlas was derived from a true holospondylous vertebra, but one in which the primitively large intercentrum was persistent; perhaps such a vertebra as is found in *Seymouria*.

Among modern reptiles a proatlas is known in the Crocodilia and *Sphenodon;* also in certain dinosaurs and the Therapsida. In *Procolophon*, as Broom informs us, the atlas and proatlas are almost identical with those of the Pelycosauria, except that the intercentra in front and behind the axis are parial, a condition also found in some modern turtles. In the *Dinocephalia*, according to the same authority, the atlas and proatlas seem to be typically pelycosaurian in structure. Indeed, it may be assumed that this condition is that of all primitive reptiles. Brown (Osteology of *Champsosaurus*) describes the arch of the atlas in the very archaic genus *Champsosaurus* as articulating directly with the exoccipital by an anterior process. This condition would be remarkable, and one wonders whether there may not have been an intervening proatlas which has not been recognized.

The *axis* (fig. 24) differs from that of *Dimetrodon* especially in the much greater antero-posterior expansion of its spine, which is even greater than in other known

poliosaurids. The spine is thickened behind, thin in front, projecting much anteriorly, and is helmet-shaped in outline. The atlantal zygapophyses in front are relatively small. The centrum differs very little from that immediately following.

Postaxial vertebræ (figs. 24–26): The centra of the first four vertebræ back of the atlas are especially characterized by the obliquity of their articular faces; this obliquity decreases on the fifth, and the centra of the following vertebræ all have their terminal articular faces nearly at right angles to their long diameters. On the first four postaxial centra the cartilaginous surface of the anterior rims is carried far back. The capitula of the ribs articulated in part on this surface, but its great extent is doubtless due to the increased mobility of the vertebræ in this region. For this reason, as also because of the position of the scapulæ in the specimen, the first six, if not the first seven, vertebræ may be considered as true cervicals.

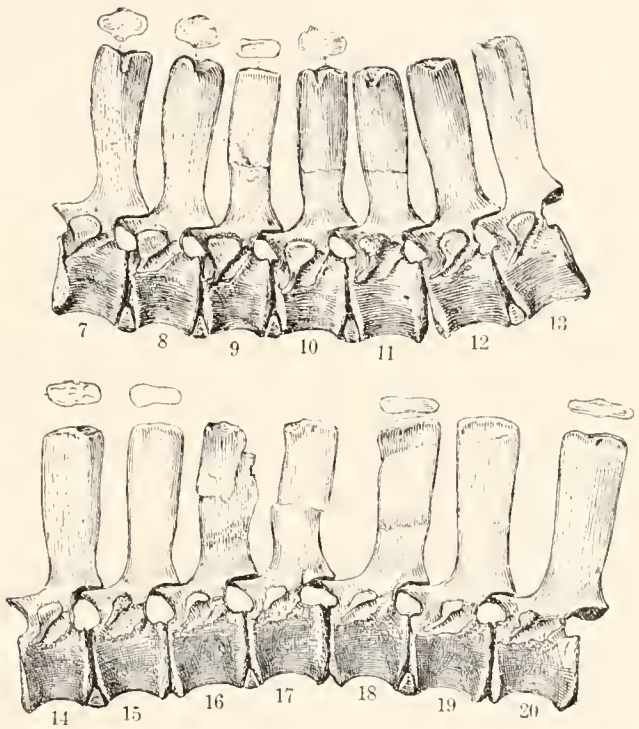

FIG. 25.—*Ophiacodon mirus* Marsh. Seventh to twentieth vertebræ from the side, × ½.

The centra of the cervical vertebræ are a trifle longer than those of the dorsal region, which are all nearly uniform in length. The under side is gently concave in outline. The anterior vertebræ have a sharp, thin keel below; in the posterior vertebræ the keel is thicker, with angular or parallel sides. The articular faces of the zygapophyses are directed at a considerable angle inward and outward. The zygapophyses are strongest in the cervical region. The spines of the vertebræ are of nearly uniform height throughout the presacral series, ascending above the centra about 2.5 times their vertical diameter, or a little more. Anteriorly, as far as the tenth or eleventh vertebra, they are stout, with a truncate, cartilaginous surface at the extremity, of an oval or ovate outline. Back of the eleventh or twelfth vertebra the spines decrease in thickness and increase in width, becoming quite thin and flat in the posterior region, as shown by the outline figures of the extremities. Very remarkably the fourth and the ninth spines, especially the fourth,

are conspicuously different from those immediately adjacent, as shown in the figures; so different, indeed, are these spines that had they been found isolated they would have been unhesitatingly referred to a different genus from that of the other vertebræ. Doubtless they are anomalies that will not be found in other specimens of the same species.

The diapophyses are very much as they are in *Varanosaurus* * and *Dimetrodon*. Those of the cervical region are stouter, and are directed outward, downward, and backward, becoming almost transverse in position in the sixth, quite as in *Varanosaurus*. Beginning with the seventh vertebra the processes project transversely, gradually becoming shorter and less stout, until in the last, that is, the first presacral, they are mere tubercles for the sutural attachment of very short ribs. In all the presacral vertebræ, unless the first three are exceptions, the articular surface for the tuberculum is continuous on a thin prolongation extending downward and forward to the intercentral space. The diapophyses are located exclusively upon the arch, as shown by distinct sutural lines distinguishing the arch from the centrum.

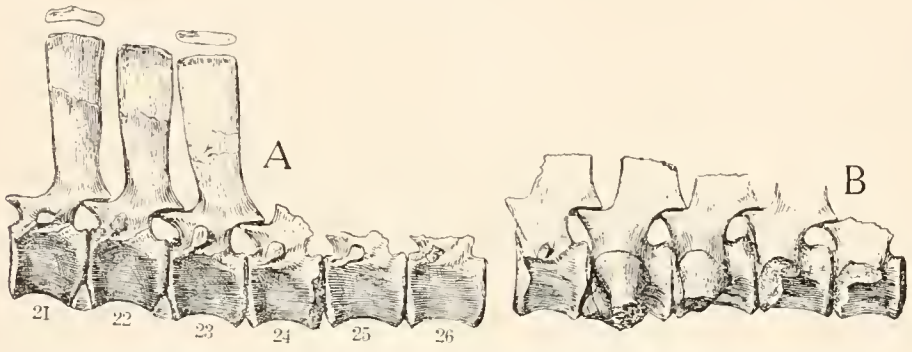

FIG. 26.—*Ophiacodon mirus* Marsh, × ½. A, twenty-first to the twenty-sixth vertebræ from the side; B, first presacral, sacral, and two proximal caudal vertebræ from the side.

The intercentra were probably preserved throughout the presacral series, but a few have been lost in the preparation of the specimen. They measure about 12 mm. from side to side and 4 mm. in width.

Sacrum: Unfortunately, as already explained, the sacrum of the more perfect specimen (No. 650) was lost in collection. Of the second specimen (No. 651) the posterior presacral vertebræ, the sacrum, and numerous vertebræ of the tail were found loosely united by matrix, though with their processes more or less broken away and lost. The sacral vertebræ, so far as they are preserved, scarcely differ from those immediately preceding, except in their ribs and rib attachments. The sutural surfaces for the ribs, shown fully on the right side, are very extensive, especially in the first of the two vertebræ. The diapophysial surface is broad and overhanging; the parapophysial surface, of less extent, reaches quite to the lower margin of the centrum at the anterior end. On the second vertebra the surfaces are less extensive, about equally divided between arch and centrum, and the ribs of both vertebræ projected at their capitular end into the intercentral space. The distal extremities of the sacral ribs of both vertebræ are lost, but a nearly complete rib found among the loose bones in the wash shows a structure not unlike that of *Varanosaurus*. There were but two pairs of sacral ribs, as shown in the figure.

Caudal vertebræ: With the more complete specimen thirteen vertebræ were found associated, connected by matrix in two series, as shown in fig. 27. From

* Williston, American Permian Vertebrates, plates I, II.

the wash of the two specimens numerous other caudal vertebræ were obtained, but it is impossible to say to which skeleton they belong; in all probability they belong with both, though there seem to be few or no duplicates. As they differ so little in their characters, only a few have been figured—the four distal ones shown in fig. 27 B. The first one shown in fig. 27 A may be either the third or the fourth of the series. The tail as a whole must have been very much like that of *Varanosaurus*, long and slender, and probably included, as in that genus, fifty or more vertebræ. Conspicuously different, however, are the numbers of pygal vertebræ, that is, those without chevrons, in the two genera. In *Varanosaurus* there are not more than three, while in *Ophiacodon* there are at least six, and possibly seven. The spines decrease rapidly in size and height, the first complete ones preserved, those of the eighth and ninth caudals, being even shorter than the corresponding ones of *Varanosaurus*. Between the two series shown in figs. 27 A and B there is, in all probability, but one vertebra missing, the perfect spine shown being that of the fourteenth or fifteenth vertebra. Between the last of this series and the next one shown in the figures, probably the thirtieth, a dozen vertebræ are preserved. The smallest vertebra figured is probably the fortieth or thereabouts, possibly the forty-fifth.

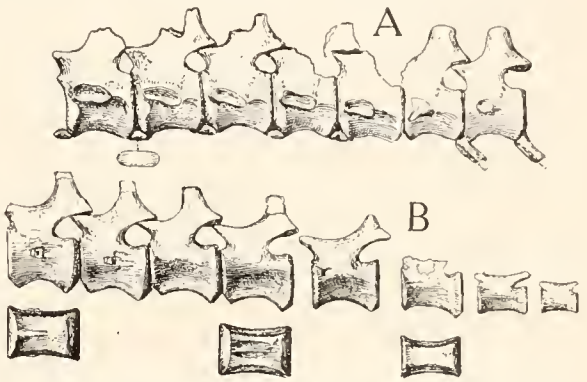

FIG. 27.—*Ophiacodon mirus* Marsh. A, proximal caudal vertebræ from side; B, proximal and distal caudal vertebræ from side, × ½.

From all of which it is quite certain that the tail was long and slender, perhaps more slender than that of *Varanosaurus*, of which forty-seven caudal vertebræ have been found in a continuous series, with at least a half dozen terminal ones missing. There are ten or more pairs of suturally united ribs, the proximal ends of many of which are yet connected with their vertebræ, but whose lengths can not be determined. This is about the number occurring in *Varanosaurus* and most other contemporary reptiles. The anterior caudal centra are rather sharply keeled below, but the under side soon becomes flat, or has a pair of grooves separated by a low keel. Evidently well-developed chevrons were present throughout the series back of the sixth or seventh, though only a few fragments of them have been recovered. The tail very clearly was not natatorial in structure.

Ribs: All the vertebræ as far back as the eleventh or twelfth caudal are costiferous. The ribs have the usual articulations of the primitive reptiles, the head resting more or less in the intercentral space, the tubercle articulating with the arch. In no presacral vertebra is there a distinct parapophysial surface on the centrum, but the tubercle articulates with a more or less prominent diapophysis. In *Ophiacodon* there is a more or less continuous articular surface between the capitulum and tuberculum, as in most of the contemporary cotylosaurs. In most of the ribs this intervening surface is narrow, and in some it is obsolete, but in none is there a distinct emargination as in other known pelycosaurs.

In many of the primitive reptiles, such as *Diadectes*, *Labidosaurus*, *Captorhinus*, *Pareiasaurus*, *Paleohatteria*, and *Sphenodon*, as also the "Microsauria," the ribs are commonly called single-headed, but incorrectly, since all have the two articular surfaces, capitulum and tuberculum, the former articulating in or near

the intercentral space, the latter with the arch at the extremity of a more or less prominent diapophysis. And this is the primitive rib attachment in reptiles. In the further evolution of the ribs these two surfaces, primitively continuous, become separated by an emargination, leaving a distinct foramen between the articulated rib and its vertebra. This modification of the articulation was, however, acquired in different phyla independently, since we find the continuous articulation, the "single-headed" rib, in such diverse reptiles as the "Microsauria," *Diadectes*, *Labidosaurus*, *Ophiacodon*, *Palcohatteria*, and *Sphenodon*, while the emarginate form, or "double-headed" rib, was acquired in such a generalized cotylosaur as *Seymouria* (fig. 28 B). In all these reptiles, however, the ribs are distinctly double-headed in the proper sense of the word, since they have both capitulum and tuberculum. Perhaps some convenient single word to characterize each type, such as *holocephalous* and *dichocephalous*, will be useful.

Ophiacodon not only has holocephalous ribs, but also dilated cervical ribs, a character (so far as known) hitherto peculiar to the Cotylosauria. Beyond the

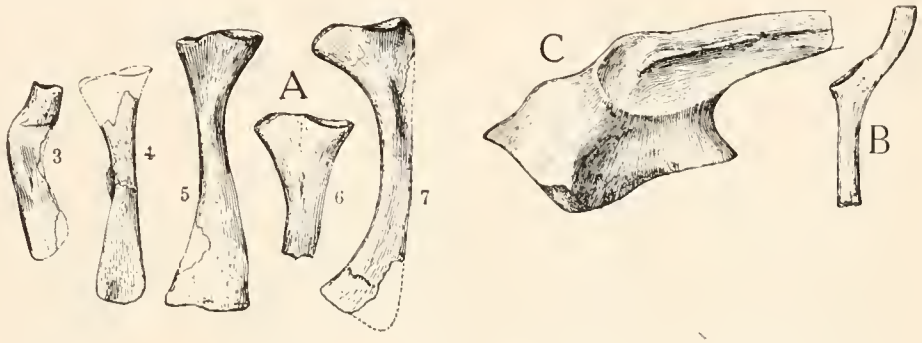

FIG. 28.—A, cervical ribs of *Ophiacodon mirus* Marsh, × ½. B, dorsal rib of *Seymouria baylorensis* Broili, × 1; C, right ilium of *Ophiacodon mirus* Marsh, inner side, × ½.

seventh the ribs are all cylindrical and slender to their extremities, becoming quite short in front of the sacrum. The first three cervical ribs, those articulating with the atlas, the axis, and the third vertebra, are short, and but little dilated distally, attached exclusively, it seems, to the diapophysis.

Ventral ribs: The size and characters of the ventral ribs are best shown in the photographic illustration (pl. 1, fig. 1). They formed a large sheet in the specimen as found, covering the whole of the space back of the coracoids and between the ends of the ribs, quite to the pelvis. They are very slender, and lie closely together, each meeting its mate in the middle in an acute V. The length of no individual rib can be determined, since they are all more or less broken into short, contiguous pieces. It is possible that some of them, if not many, were continuous throughout their whole lengths.

Pectoral girdle and extremity: The pectoral girdle and both anterior extremities lay quite in natural arrangement as found in the specimen, except that the right scapula had been pushed downward and a little forward, an inch or two from its natural place; and the left hand was partly concealed beneath the posterior dorsal vertebræ. The right arm and hand, closely articulated throughout, were directed downward and forward; the inner fingers were doubled under the outer, ulnar ones.

The *interclavicle*, preserved in place, has a broad, thin, flattened stem, somewhat convex below, and a moderately dilated anterior extremity. The stem extends backward, as articulated, about an inch beyond the posterior angles of the coracoids. In the present specimen (No. 650) it is somewhat flattened by pressure;

in life it doubtless had a considerable convexity below, the front end turned upward. The dilated end is concave above, convex below, and grooved on each side for the attachment of the clavicle.

Clavicles: Both clavicles are entire and firmly attached to the interclavicle, but are compressed and somewhat distorted. Figures 29 B and C have been made from an isolated specimen which agrees perfectly and is undistorted. As seen, the mesial extremity is only a little dilated in comparison with the clavicles of both *Varanosaurus* and *Dimetrodon*. Of this extremity, the upper side is moderately concave, the lower convex, and both sides have conspicuous radiating ridges and grooves, more pronounced near the margins. The slender stem turns upward and outward, in the articulated position, at an angle of about 130 degrees. As articulated, the upper ends are about 125 mm. apart. The front border is thickened throughout; the posterior border of the dilated part is thin. Beyond the dilated

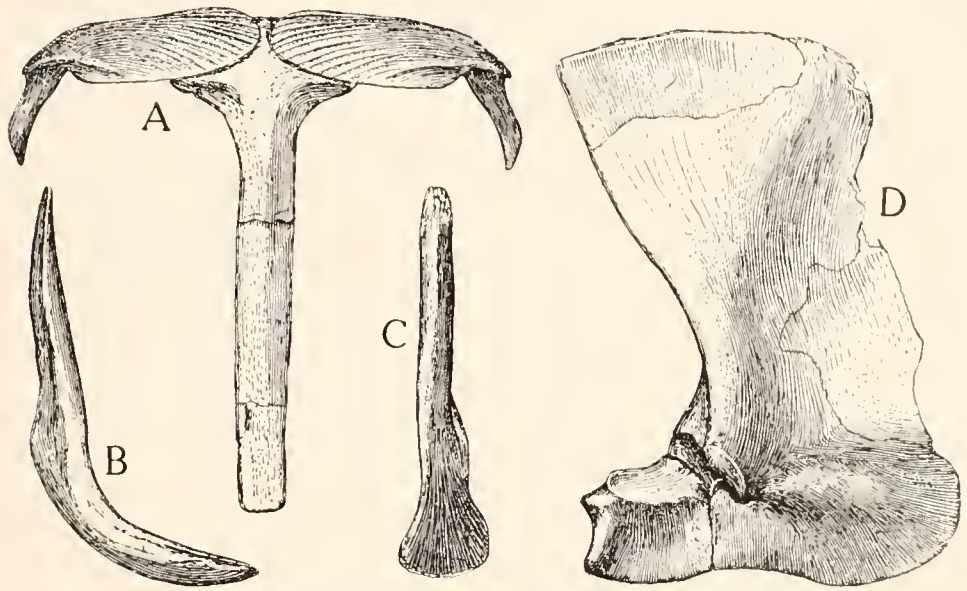

FIG. 29.—*Ophiacodon mirus* Marsh, × ½. A, clavicular girdle from below; B, right clavicle from in front; C, right clavicle from within; D, right scapula-coracoid, outer side.

part, on the posterior side, there is an everted, thin flange, which overlaps the lower front border of the scapula. Distally the shaft for a short distance is oval in cross-section, the posterior border only a little thinner and without a surface for attachment to the scapula. Still more distally the outer anterior side is flattened and grooved, and striate, as though for the articulation of a slender cleithrum, of which, however, no definite evidence has been found in the specimen.

Scapula-coracoid: The scapula-coracoid of the right side is very little distorted (fig. 29 D). The front border of the scapula, however, was so intimately united to the clavicle that it could not be recovered entire. On the left side the scapula lay over the humerus in part, and was pressed outward in its middle portion; its outline, however, was complete, and it has been used to complete the figure as shown. On both sides the scapulæ lay nearly or quite in position in the skeleton; that of the right side had been pushed downward and forward an inch or two beyond the position occupied by the left one, whose distal margin crossed the base of the spine of the eighth vertebra.

The scapula is broad, resembling that of *Dimetrodon* more than that of *Varanosaurus*. The posterior border is thickened and rounded, and curves upward and backward. The supraglenoid fossa is broad and shallow; it is pierced by the usual supraglenoid canal. The front border is thinned throughout; it is straight near the middle for about an inch, where the distal end of the clavicle is apposed. Both above and below this straight border there is a shallow emargination of the very thin bone. That a small cleithrum was present is possible, but not certain. Lying just above the end of the left scapula is a small, thin bone, so closely applied to the vertebræ that it could not be detached; it may be a vestigial cleithrum. The upper or distal border of the scapula, as usual, is truncated and convex in outline, for the attachment of a suprascapular cartilage. The coracoid of Williston, the procoracoid of authors, is narrow and, in its somewhat flattened condition as preserved on both sides of this specimen, is not directed inwardly as much as in other forms. The broad stem of the interclavicle filled a part of the interval between the two bones, but it seems probable that in life there was a considerable cartilaginous continuation of the truncate margin of each coracoid. The posterior coracoid, or metacoracoid of Lydekker and Williston, the coracoid of authors,* is of considerable size, its separating suture showing conspicuously on both sides; the suture between the anterior coracoid and the scapula is not distinguishable.

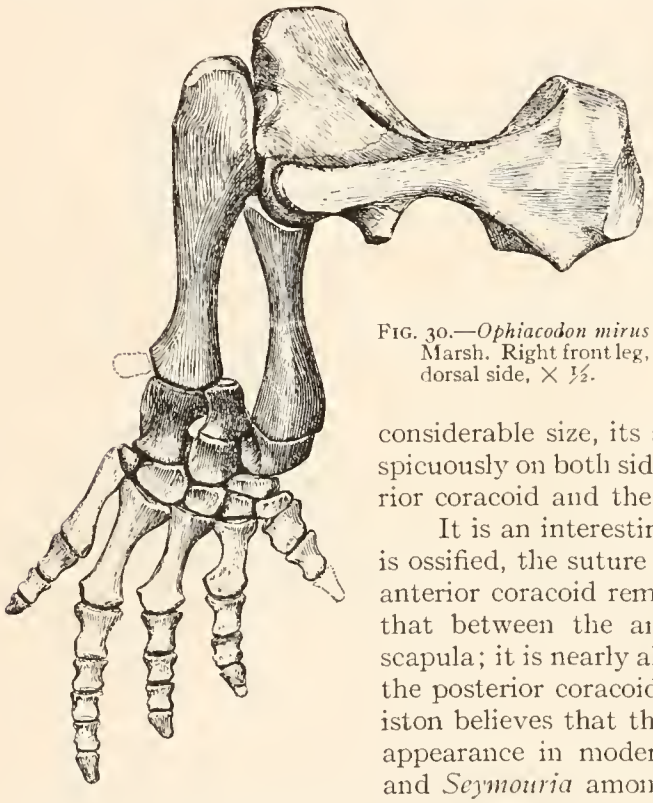

FIG. 30.—*Ophiacodon mirus* Marsh. Right front leg, dorsal side, × ½.

It is an interesting fact that, wherever this bone is ossified, the suture uniting it with the scapula and anterior coracoid remains distinct much longer than that between the anterior coracoid bone and the scapula; it is nearly always visible in *Dimetrodon*, and the posterior coracoid is often found isolated. Williston believes that this is further evidence of its disappearance in modern reptiles, as in *Varanosaurus* and *Seymouria* among the ancient ones. The bone, whatever it may be, coracoid or metacoracoid, agrees closely with that of *Dimetrodon*. Its suture passes through the postglenoid facet a little in front of its middle, and not far back of the preglenoid facet, and about half an inch posterior to the supracoracoid foramen. Its posterior border is thickened, concave in outline, and somewhat everted. At the upper part of this border and somewhat inward from the posterior end of the glenoid facet, there is a prominent process, like that of *Dimetrodon*, *Casea*, *Champsosaurus*, etc. On the inner side of the scapula is the usual subscapular fossa, with the opening of the supraglenoid foramen at its upper, that of the supracoracoid at its lower end.

Humerus: The humerus is an unusually short and stout bone for a zygocrotaphic reptile, resembling somewhat in its general characters those of *Diadectes* and *Limnoscelis*. It has a very broad entocondyle, a very large, hemispherical capitel-

* For a discussion of the homologies of coracoids, see Broom, Anatom. Anzeiger, Band 41, p. 625, 1912.

lum, and a stout ectocondyle directed obliquely dorsad. The plane of the upper extremity is relatively but little divergent from that of the lower. The rather broad, spiral, and concave glenoid articular surface winds about the bone from the dorsal outer side to the ventral inner side (fig. 31 A), and fits very perfectly into the glenoid cavity of the scapula. As articulated with the scapula, the humerus has a somewhat obliquely upward, outward, and backward position, showing conclusively that the animal in life could not have raised itself very high above the ground. Indeed, the humerus could not have been brought much below a horizontal position in life without partial dislocation from the scapular socket. The lateral process is stout and is situated at about the junction of the upper and middle thirds of the bone; in the articulated position of the humerus it was directed downward and a little forward. There is a small median process or eminence. The ectepicondylar process is stout and protuberant, directed downward and forward in the articulated position of the bone, and is situated a little beyond the middle of the distance between the lateral process and the distal extremity (fig. 31 B). The capitellum is unusually large, nearly circular in outline, and comprises about one-third of a sphere; the plane of its base is directed forward at an angle of about 45 degrees. The very stout ectocondyle is directed dorsad at an angle of almost

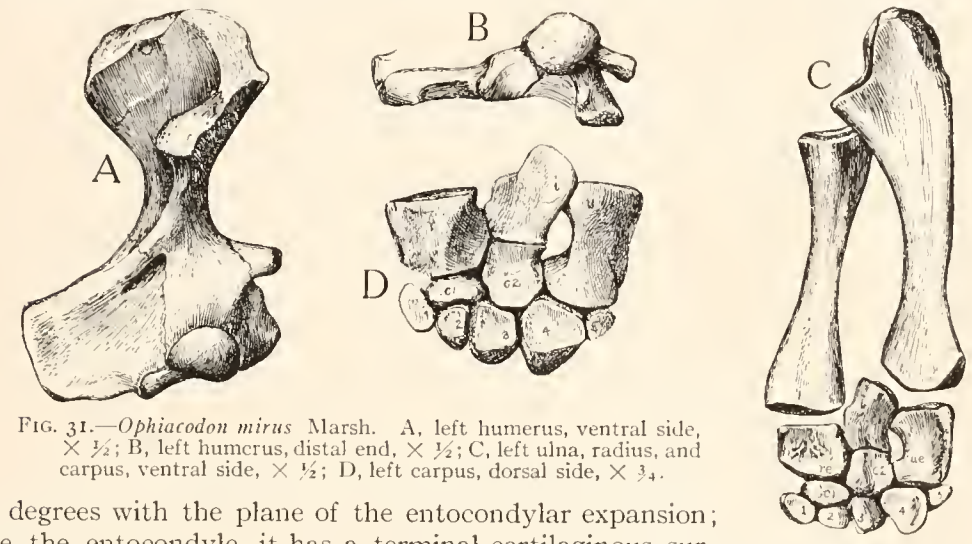

FIG. 31.—*Ophiacodon mirus* Marsh. A, left humerus, ventral side, × ½; B, left humerus, distal end, × ½; C, left ulna, radius, and carpus, ventral side, × ½; D, left carpus, dorsal side, × ¾.

90 degrees with the plane of the entocondylar expansion; like the entocondyle, it has a terminal cartilaginous surface for the attachment of powerful extensor muscles. This unusual dorsad inclination of the condyle is very characteristic of short, stout legs, and especially of short humeri, as seen in *Diadectes*, *Diasparactus*, and *Limnoscelis*. The entocondyle is very broad, and has an extensive surface on the distal border for the attachment of strong flexor muscles. The articular surface for the ulna winds obliquely about the distal border from the margin of the capitellum inward.

Altogether the prominent and stout lateral processes, the protuberant ectepicondyle, probably for the attachment of the supinator muscle, and the dorsad inclination of the ectocondyle indicate a powerful muscular control of the arm and hand, very much greater than is seen in either *Dimetrodon* or *Varanosaurus*.

Radius: The radius (fig. 31 C), about three-fourths the length of the humerus, has stout extremities and a relatively slender shaft. The truncated upper end is subtriangular in outline, with its dorsal angle rounded and its articular surface gently concave. The posterior surface above is flattened from side to side obliquely inward; the dorsal surface is strongly convex. The somewhat obliquely truncate

distal end is broadly subtriangular, with the dorsal angle rounded, the inner angle more acute. The two sides of the bone are nearly symmetrically concave in outline.

Ulna: The ulna (fig. 31 c) is a longer and stouter bone than the radius, and is almost or quite the length of the humerus. The olecranon is considerably produced, and has its distal cartilaginous surface continuous with that of the sigmoid fossa. Here, again, it is evident that the triceps was unusually powerful and that its action was exerted at much mechanical advantage. The inner border of the bone is deeply concave and is thicker than the outer or radial border. The distal extremity, somewhat less expanded than that of the radius, has its truncated articular surface for union with the carpus oblique to the long axis of the bone. Its inner angle is convex, evidently for articulation with a pisiform bone, which, however, has not been found. The ventral side of the bone is gently concave longitudinally above, convex distally.

Carpus: The carpus was found in almost perfect articulation on the right side; the bones forming it on the left side were slightly displaced. On each side the carpus has been restored so perfectly to its original condition that scarcely anything more could be desired. The number and arrangement of the bones are quite as in *Dimetrodon* and also as in *Varanosaurus*, except that the first centrale and the fifth carpale are well ossified in *Ophiacodon*. The radiale is a short, thick bone, very convex in front. The intermedium is elongate and helps to form a half of the articular surface for the ulna. The ulnare is also elongate and rather narrow; its inner margin curves ventrad. The perforating foramen is rather large, formed by the ulnare, intermedium, and second centrale. Of the five carpalia the fourth is the largest, as usual, the third is next in size, the fifth is small, and the second is not much larger. The first centrale is intercalated between the radiale, second centrale, and first three carpalia. The second centrale is larger, articulating with all the bones of the carpus except the first and fifth carpalia. The carpus, as articulated, is convex from side to side on the dorsal side, concave on the palmar. The articulations of the radiale, intermedium, ulnare and second centrale are all close, permitting little motion between them. The articulations of the first centrale and all the carpalia are loose, not only with each other, but also with the bones of the first row, especially so on the radial side of the wrist; the free surface of the first centrale is broader behind than in front.

Hand: The bones of the right hand were all found in intimate articulation with each other and with the carpus, save the distal two phalanges of the thumb, which doubtless were lost in collection. Of the left hand the distal phalanges of several fingers could not be found, but the proximal phalange of the thumb was in position, giving the complete structure of the hand, with the exception of the ungual phalange of the first digit. The thumb metacarpal is, as usual, small and broad; the second, third, and fourth metacarpals increase markedly in length, but not nearly so much so as do the corresponding ones of *Varanosaurus*. The fifth metacarpal is about two-thirds the length of the fourth; it is slender and curved, and was evidently divaricable in life; possibly, as in many lizards, it was freely separable in life to the base of the metacarpal. The ungual phalanges differ markedly from those of other known American Pelycosauria or Theromorpha in their less curved and less pointed form. They are more like nails than claws, almost flat on the under side, somewhat thinned at the extremity, but not at all pointed. The animal could have made no use of them in climbing, or as offensive or defensive weapons.

In figure 30 the right arm and hand are shown almost precisely in the position in which they were found in the matrix, save that some of the digits have been straightened out and a few of the loosened carpal bones have been more closely adjusted. A

plaster cast of the arm and hand was made before removal from the matrix. After removal from the matrix the bones were placed in the mold and cemented together in that position, a position shown to be quite natural by the articular surfaces. The divarication and curves of the fingers have been given as demanded by the articular surfaces. The elbow, it is seen, is strongly bent, and it seems certain, because of the humeral and epipodial articular surfaces, that this flexure was the usual one in life; complete extension of the forearm would have been impossible.

Pelvic girdle and extremity: The *pelvis* of specimen No. 650 was somewhat injured in collection, but enough remains to show its absolute identity in characters and size with that of specimen No. 651, of which only the ilium and ischium of the right side are missing. The pelvis is distinctly of the true pelycosaur type, but is especially characterized by the massive sutural union of the pubes.

The *ilium* (fig. 32 A, *il*) agrees quite with that figured by Williston in his American Permian Vertebrates (plate XXXVII, figs. 4, 5) and there tentatively referred to *Ophiacodon*. It has a long and slender posterior prolongation, in part wanting in the present

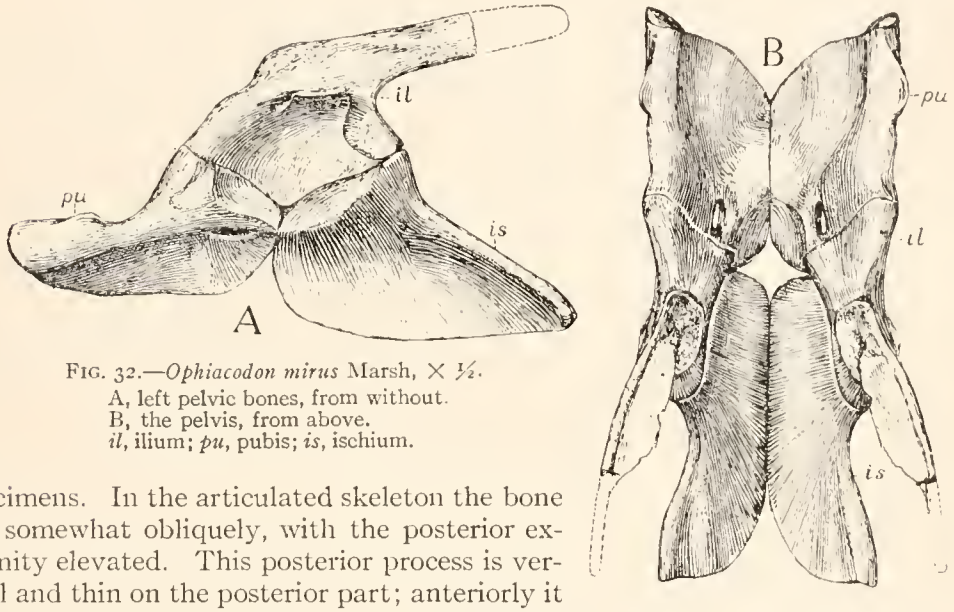

FIG. 32.—*Ophiacodon mirus* Marsh, × ½.
A, left pelvic bones, from without.
B, the pelvis, from above.
il, ilium; *pu*, pubis; *is*, ischium.

specimens. In the articulated skeleton the bone lies somewhat obliquely, with the posterior extremity elevated. This posterior process is vertical and thin on the posterior part; anteriorly it has a transverse thin shelf or plate, jutting inward. The articular surfaces for the sacral ribs are at the anterior end of this shelf, partly in front, partly below, forming an oval excavation and showing a strong union with the ribs. The sutural borders for union with the pubis and ischium are strong and massive, meeting a little below the middle of the acetabulum in rather more than a right angle, that for the ischium a little longer than that for the pubis. On the inner side the convex thickening which joins the posterior end of the pubic symphysial thickening limits the brim of the true pelvis, the false pelvis extending far in advance.

The *pubis* (figs. 32 and 34 B) projects strongly forward, with a heavy lateral bar, curved somewhat inwardly. On the margin of these bars, on the outer side at about the middle, there is a thin, everted pectineal process. The two pubes meet in a very thick and strong median symphysis very unlike that of either *Dimetrodon* or *Varanosaurus*, where the general shape of the pubis is nearly the same. The two articulated bones extend far in front of the brim of the true pelvis, as a sort of shallowly concave, nearly horizontal trough, supported on its sides by the thickened bars. Back of the broad symphysis the two bones together form a concave,

rather deep spout leading into the narrow and deep concavity formed by the ischia. The perfect condition of the two pubes of specimen No. 651 permits an accurate coaptation of the whole pelvis, an upper view of which is shown in fig. 32 B. The true pelvis, it is seen, is narrow, the greatest diameter of its brim being scarcely more than an inch, and its depth is less than 2 inches. And this is the outlet through which the eggs of a creature nearly 6 feet in length must have passed. The obturator foramen pierces the pubis in its usual place. Between the pubes and the ischia, as articulated, there is a diamond-shaped pubo-ischiadic vacuity of moderate size, as in all the true pelycosaurs.

The *ischium* (fig. 32) is of the usual shape, an elongated, hatchet-shaped bone meeting its mate in an acute angle below. Its upper posterior border is thickened and everted, and there is an angular excision between it and its articulated mate behind.

What the significance of the peculiarly elongated and horizontal expansion of the pubes is we can not suggest; that it has something to do with the habits of the

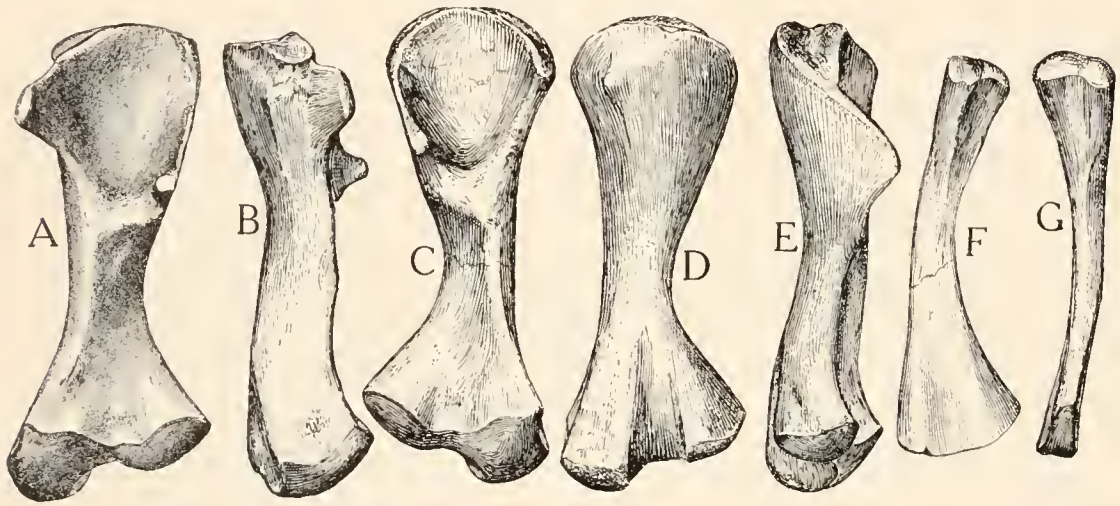

FIG. 33.—*Ophiacodon mirus* Marsh, × ½. A, left femur, ventral surface; B, left femur, fibular side; C, right femur, ventral side; D, right femur, dorsal side; E, right femur, tibial side; F, left fibula, ventral side; G, left fibula, tibial side.

animal seems probable. In the present genus the massive symphysis between the pubes indicates a firm and strong pelvis, one able to sustain a considerable weight. In *Limnoscelis* the massive symphysis extends through both pubes and ischia; in *Seymouria* the pubic symphysis is weak, while that of the ischia is deep; in both *Dimetrodon* and *Varanosaurus* the symphyses of both ischia and pubes are slight.

Femur: The femur is relatively stout, its extremities considerably expanded. The digital fossa extends a full third of the length. The trochanter stands out prominently, but ends abruptly, not continuing into the adductor ridge. Below the trochanter, on the fibular side, there is a distinct roughening for the attachment of muscles. The tibial condyle projects strongly inward from the longitudinal axis of the bone, its articular surface looking inward at an angle of about 45 degrees. As usual, the fibular condyle has much the larger articular surface, which is connected by a narrow band on the ventral side with that for the tibia. Neither surface can be seen broadly from the dorsal side, indicating a normally much flexed knee in life. The left femur (fig. 33 A) has a remarkable anomaly: On its fibular side (fig. 33 B) the proximal articular surface is broad and has a distinct rim separating it by a considerable interval from an elongate oval cartilaginous surface at the

extremity of a thin, elongate process directed ventrad and laterad. This surface doubtless corresponds to the outer end of the cartilaginous surface of the proximal end, though separated by a thin, non-cartilaginous interval; and it is very much more protuberant. The trochanter on the tibial side is unusually produced ventrad; its lower border also is situated further down the shaft, and its extremity is smaller. In other respects this femur does not differ from its mate.

Tibia (fig. 34 A): The tibia is rather more than four-fifths the length of the femur. It is a rather stout bone, with its upper extremity much expanded. The articular surface for the tibial condyle is elongate and crescentic in shape, separated by a ridge and groove from the rather large surface of an oval shape which articulates with the posterior side of the fibular condyle of the femur.

Fibula (fig. 33 F and G): The fibula is a little longer than the tibia. It has a rather slender shaft, and the lower end is much expanded. The upper end is mod-

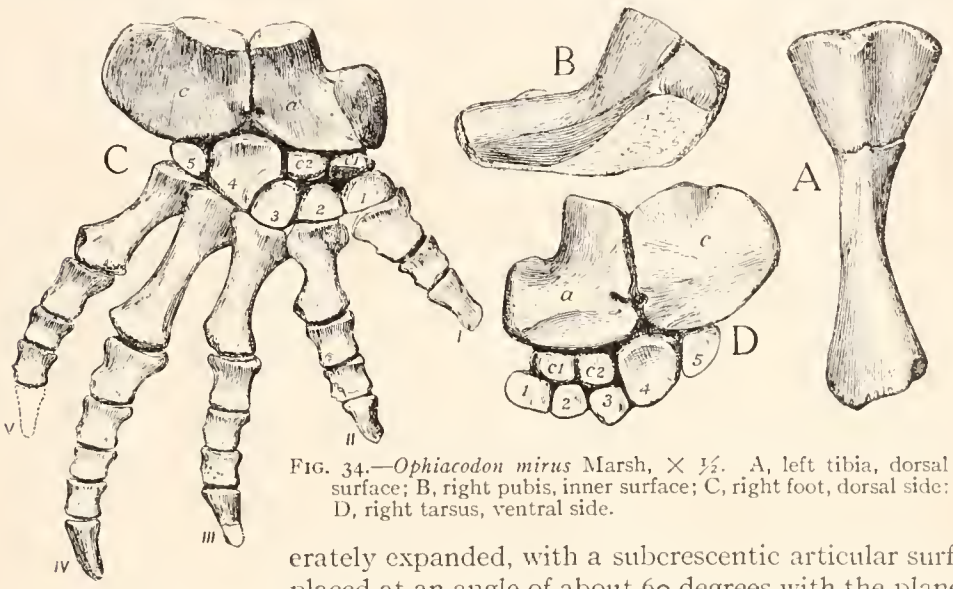

FIG. 34.—*Ophiacodon mirus* Marsh, × ½. A, left tibia, dorsal surface; B, right pubis, inner surface; C, right foot, dorsal side; D, right tarsus, ventral side.

erately expanded, with a subcrescentic articular surface placed at an angle of about 60 degrees with the plane of the lower end. Its articular surface fits well the elongate, curved articular border of the femoral condyle, sliding, in articulation, forward and inward and backward and outward; that is, in the extended condition of the leg, the plane of the distal extremity is horizontal, while in the much-flexed condition this plane is turned obliquely. The outer border of the bone is nearly straight, the inner border deeply concave to the lower end. The truncate border is gently curved on the inner side for articulation with the astragalus.

Foot: The right foot of specimen No. 650 (fig. 34) lay in the matrix with most of its bones in close articulation. The first three digits were doubled under the others, but had all their phalanges attached; one claw, only, was lost in the collection of the specimen. Of specimen No. 651, the left foot was nearly as perfect, the calcaneum and centralia missing.

The *tarsus* has the same general structure as have the tarsi of other American zygocrotaphic reptiles, except that there are two free centralia instead of the single one hitherto known. The calcaneum is broad and flat, subcircular in outline, with its free borders thin. The astragalus is rather more elongate than usual, and its tibial facet is separated rather widely from the fibular one. The perforating foramen between the two bones opens near the distal end of the articulating borders. The two centralia were found quite in position, as were all the other bones of the

tarsus save the first two tarsalia, which, with their respective toes, had been pulled a little distance away from the others. They articulate between the astragalus and the first two tarsalia and have their free surfaces in front much less extensive than those behind, indicating the possibility of considerable over-extension of the inner toes and corresponding tarsalia upon the proximal ones. The fourth tarsale is, as usual, considerably the largest, and the fifth is the smallest. In fig. 34 C the tarsus is shown in the oblique position of life; in fig. 34 D it is shown from behind, lying horizontally, the surface somewhat convex. This convexity is that in which the bones were found in the matrix, and the position is that assumed in articulation; evidently it was the normal articulation of the foot in life, and it is doubtful whether the foot could have been straightened out in the same plane with the bones of the leg.

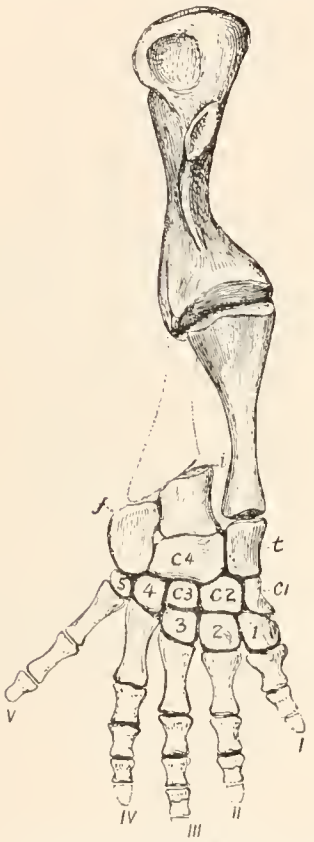

FIG. 35.—*Trematops milleri* Williston. Left hind leg, ventral side. Reduced.

The curvatures of the toes, as shown in fig. 34 C, are quite those which the metatarsals and phalanges assume in close articulation with each other. The first metatarsal is, as usual, short and broad; its proximal articular surface is of considerable extent and is convex, both dorsoventrally and transversely, showing conclusively that the toe was capable of much over-extension as well as of much free lateral movement. On the other hand, the third and fourth metatarsals, of much greater length, fit closely at their proximal ends with their respective tarsalia, and were not capable of much movement, either laterally or dorsoventrally. The second metatarsal, of considerably greater length than the first, had also much freedom of movement in both directions, as had also the fifth metatarsal. The distal end of the astragalus has a much greater extent of surface than the sum of the opposing surfaces of the centralia, indicating a considerable arthrodial action between them. The ungual phalanges are more nail-like than claw-like; they are thin and flattened, and even somewhat dilated at their tips. They are scarcely curved and are not pointed.

The foot was broad and flat, one well adapted for soft or uneven ground, but quite unfitted for climbing or running. The posture of the leg shown in the restoration is clearly a natural one. The articular surfaces are sharply and clearly defined.

This tarsus of *Ophiacodon*, the most generalized known among reptiles, may be compared with that of *Trematops*, a contemporary temnospondylous amphibian, as shown in the accompanying figure, after Williston (fig. 35). The astragalus, it is seen, corresponds quite in its relations with the combined tibiale, intermedium, and fourth centrale of the amphibian, with the perforating foramen at the junction of the intermedium and centrale with the fibulare, precisely as in the carpus. The first and second centralia of the reptile likewise correspond with the first two centralia of the amphibian, each supporting its respective tarsale. The third centrale plus fourth tarsale of the amphibian tarsus also occupies the place of the enlarged fourth tarsale in the reptile.

NOTE BY WILLISTON.—The tibia in figure 35 is shown precisely as it lies in the matrix in articulation with femur and tarsus. In the original figure the fibular side of the tibia is shown, in the belief that the bone had suffered rotation. Such rotation, however, did

not occur, since the side shown in the present figure corresponds quite to the ventral side as determined since in various other forms. The foot lies nearly in the position as regards the leg that is shown in the present figure; possibly in life it was angulated more to the tibial side, leaving more room for the fibula, which is unknown. The arrangement of the bones of the tarsus agrees well with the observations of Baur on *Archegosaurus*, who, however, remained in doubt as to the presence of a fourth centrale.

Concerning the homologies of the tarsal bones in the reptiles, there has been not a little dispute, and the subject is by no means yet at rest. Gegenbaur, in 1864, considered the astragalus of mammals as a composite formed by the fusion of the tibiale and the intermedium, and this view is the one usually accepted at the present time. Baur, however, (Morphologisches Jahrbuch, XI, 468), after a careful examination of the embryos of numerous reptiles and mammals, reached the conclusion that the astragalus is a single element, with no evidence of fusion; that, in the Prototheria and Eutheria at least, "ein Intermedium tarsi niemals embryologisch nachweisbar ist." Among certain marsupials only, and as an occasional anomaly in the human foot, a small bone is found wedged in between the astragalus, tibia, and fibula at the back part of the ankle joint, which Bardeleben believed to be the intermedium, but which Baur was disposed to consider a neomorph or sesamoid. In the belief that the astragalus represents but a single bone, which he was inclined to consider the intermedium, Baur recognized in the "tibial sesamoid" the real tibiale. This "tibial sesamoid" is a bone not infrequently found in mammals, but unknown in reptiles, on the tibial side of the tarsus, articulating with astragalus, navicular and internal cuneiform. Baur gave four hypotheses: First, that the tibiale is represented by the tibial sesamoid, the intermedium by the marsupial sesamoid of Bardeleben; second, that the tibial sesamoid is the tibiale, and the astragalus wholly the intermedium; third, that the tibial sesamoid is the first tarsale, the marsupial bone the intermedium, and the astragalus is the tibiale; fourth, that the tibial sesamoid and the marsupial bones are real sesamoids, and the astragalus is the combined tibiale and intermedium. Although Baur recognized the possibility of four free centralia in the amphibian foot, he did not recognize the possibility of more than one in the reptilian tarsus, since none is known in any recent reptile, nor more than one in any reptile hitherto. It seems to me that the presence of two free bones between the astragalus and the inner tarsalia in the present genus offers an explanation of the "tibial sesamoid," if it be necessary to derive the bone from a true tarsal element. The first of these centralia occupies the position of the sesamoid bone in the mammals, nearly, and it is not at all impossible that its presence may have been continuous in that phylum from which the mammals arose.

In a previous paper (Amer. Permian Vertebrates, p. 44) I have expressed the opinion that a free intermedium tarsi is never present in adult reptiles as a distinct bone, as based upon the fact that in all the earliest-known reptiles, from the Middle Pennsylvanian to the Trias, there are but two bones in the proximal row of the tarsus, bones corresponding quite to the astragalus and calcaneum. Nor can I find in any later reptile, either extinct or living, any certain evidence of its presence. We may safely say that if the intermedium once had disappeared in the ancestral forms it never reappeared as a normal functional element in their descendants. Any other interpretation of the known facts would require the existence of two distinct phyla of vertebrates, beginning nearly as early as the Mississippian, and continuing without break to the present time—one in which the intermedium had disappeared, the other in which it was persistent, but of which we have yet found no certain representatives.

Schmalhausen (Anat. Anzeiger, 1908, p. 378), from the study of pig embryos, reached the conclusion: "dassbei den Vorfahren der Säugethiere mindestens eine Dreizahl der Centralia Tarsi vorhanden war; das eine proximale ist jetzt im Astragalus mit dem Intermedium zusammen eingeschlossen, das zweite ist im Naviculare erhalten, und das dritte kann, wie bei Schweine, mit dem Cuboid verschmelzen." The tibiale, according to him, has disappeared, or is represented by the vestigial sesamoid. On the other hand, Broom declares that the astragalus is composed exclusively of the tibiale, because he finds in *Oudenodon* a small bone occupying the position of a vestigial intermedium, possibly corresponding to the bone found in the marsupials.

It is generally assumed that the fourth tarsale of modern mammals is a compound bone formed by the fusion of the fourth and fifth tarsalia. There is no embryological evidence of such fusion, and with Sewartseff (Anat. Anz., 1904, p. 483) and Baur I believe that the fifth tarsale has entirely disappeared in all modern vertebrates. It is an actual fact that in some Permian reptiles the fifth tarsale is gone, not fused, but disappeared as a bone. I am not one of those who must find in the human skeleton distinct ossificatory or even embryological evidence of every lost bone that has existed in ancestral forms. In some cases it is quite certain that bones do fuse; the temporal and frontal bones of mammals, to say nothing of the opisthotic, etc., are sufficient evidences of the fusion not only of cartilage bones, but membrane bones as well. But, in many cases, it is equally evident that bones actually disappear. Possibly they remain as potential or latent elements, as mere germs, which under stimulation in later forms may develop sporadically into a semblance of their original forms, such as some of the accessory or anomalous bones found in the human carpus and tarsus, the centrale carpi or the cuboides secundarium for instance. And yet, it would seem that we are going a long way back, to the Trias or Permian perhaps, to find the normal functional prototypes of some of these germs. Indeed, if we must find the functional antecedents of all the anomalous bones found in the human carpus and tarsus we shall have to go back quite to the Stegocephalia, if not the fishes. It seems to me more probable that many of such anomalies are to be explained by duplication, by the splitting or division of normal germs, as we know is quite possible.

RESTORATION.

The accompanying restoration, made with painstaking care (fig. 36), and the mounted skeleton as shown in the photographic illustration (pl. 1, fig. 3) have very little that is conjectural or even doubtful. The spines of the posterior lumbar,

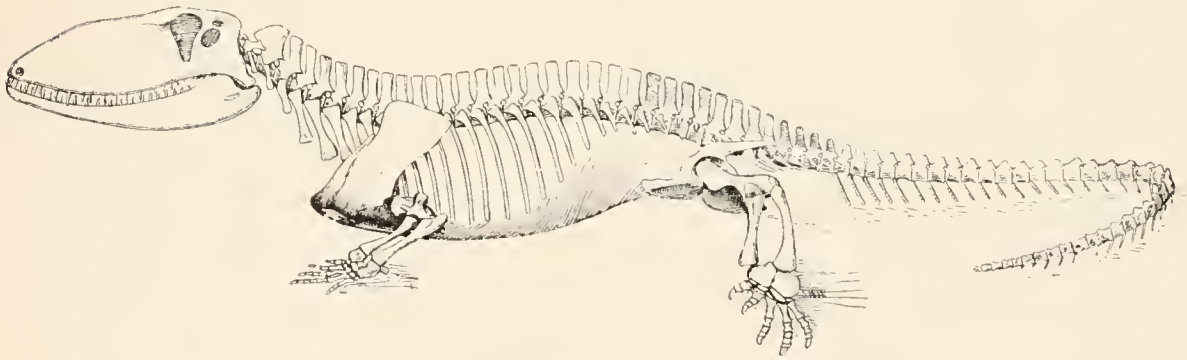

FIG. 36.—Skeleton of *Ophiacodon mirus* Marsh as restored. About one-tenth natural size.

sacral, and the basal caudal vertebræ are unknown; they are shown in the drawing by barred outlines; in the mounted skeleton they are restored in light-colored plaster-of-paris. Enough caudal vertebræ from different parts of the tail are known to render it certain that it was very much like that of *Varanosaurus*, that is, slender and nearly as long as the presacral region. It was doubtless composed of about fifty-five vertebræ, of which about twenty are wanting. The chevrons are represented by fragments only. The scapula is placed very nearly as the left one was found lying in the specimen. The right scapula lay immediately over the left one, save that it had been pushed downward a short distance. The curvature of the vertebral column in the cervical and dorsal region as found, and as shown in pl. 1, fig. 2, which is a photograph of a cast of the specimen as it lay in the matrix, is perhaps a little exaggerated, though doubtless normal, since all the vertebræ lay in immediate contact and without noticeable displacements. The curves, however, are probably not those often assumed in life; they have been reduced a little in the figure. The skull in the mounted skeleton

1. Ophiacodon retrorsus Marsh. Ventral view, natural size.
2. Same. Specimen No. 950 University of Chicago, as found in matrix, reduced one-half.
3. Same. Skeleton restored. About one-sixth natural size.

has been left in matrical association with the cervical vertebræ. The ventral ribs are figured as nearly as possible as they were found on the left side, the under side as the skeleton lay in its matrix, filling up most of the open space below the ribs in front of the pelvis and extending forward quite to the hind end of the interclavicle. It is evident that there was no cartilaginous sternum in life back of the coracoids.

HABITS AND RELATIONSHIPS.

The relatively large size of the skull of *Ophiacodon* is very conspicuous in the restoration. It is quite a third of the length of the body to the base of the tail, and doubtless more than a sixth of the entire length of the creature. It was very narrow and high, and had an inconsiderable weight in life, notwithstanding its length, composed as it is of very thin and delicate bones. The nostrils and eyes were relatively small, though quite large enough for the body. The legs are short and stout, with broad feet and flattened ungual phalanges; and the tail was slender throughout. Without taking into account the character of the claws, it is evident that *Ophiacodon* was neither a swimming nor a burrowing animal; its tail would have been of no use in the water in propulsion; and the front legs were not nearly long enough to excavate a hole for the head to enter. And it is also apparent that *Ophiacodon* was not a swift-moving reptile. Doubtless, like so many of its congeners, it spent its life about the flat marshes and low plains, feeding upon such small reptiles and amphibians as it could capture—which did not require much speed, since nearly all were sluggish creatures—possibly varying its diet with soft-bodied invertebrates. Its long, slender and recurved teeth were well adapted for the capture of slippery creatures, but, with the jaws, they were too weak to withstand much struggling of strong-bodied prey.

Aside from *Theropleura*, the relationships of *Ophiacodon* are not very intimate with any known reptiles. That it should be located in the same suborder with the true Pelycosauria seems altogether reasonable, notwithstanding the paired temporal vacuities and the holocephalous ribs. The pelvis, especially, has the very characteristic elongation of the pubes, projecting far in advance of the true pelvic brim; and the puboischiadic vacuity is as in *Dimetrodon* and *Varanosaurus*. The two sacral vertebræ, a not very profound taxonomic character, allies the form with the Poliosauridæ. The relatively short spines, of uniform length, are like those of *Varanosaurus* and its allies, though, unlike them, the anterior ones are thickened, doubtless for the better support of the elongated head. That the extraordinarily elongate spines of *Dimetrodon* is a very important taxonomic character does not seem as probable as formerly, since there is now but little doubt that the spines of *Sphenacodon* are not unlike those of *Ophiacodon*, though the skull and dentition seem to be quite like those of *Dimetrodon*.

It is very probable, if not certain, that the genus *Theropleura*, from the Texas beds, is a closely allied, if not identical genus. The vertebræ, limb bones, and such parts of the skull as are known, as figured by Case (Carn. Inst. Wash. Pub. No. 55, pls. 3 and 13) all resemble the corresponding parts of *Ophiacodon* closely. Mandibles and maxillæ from the Craddock bone-bed in Texas, mentioned by Williston as probably belonging in a new genus,* are also very like the same parts in *Ophiacodon*, save that the teeth are more compressed.

If *Ophiacodon* and *Theropleura* are eventually found to be closely allied but distinct genera, it may become advisable to separate them into a distinct family, the Ophiacodontidæ. For the present they may both find a place in the family Poliosauridæ.

* American Permian Vertebrates, p. 75.

A DESCRIPTION OF SCOLIOMUS PUERCENSIS, NEW GENUS AND SPECIES.

By S. W. Williston and E. C. Case.

A new genus of pelycosaurian reptiles is represented by some remains (No. 656 University of Chicago) found by Dr. v. Huene in the vicinity of Arroyo de Agua on the Puerco in New Mexico. The specimen consists of a complete left humerus, the two ends of the right humerus, the proximal end of an ulna, a nearly complete left femur, the proximal end of its corresponding tibia, a centrum, and a few fragments.

The genus is especially characterized by the unusual divergence of the planes of the proximal and distal ends of the humerus. Usually, among Paleozoic reptiles, the plane of the proximal end diverges from that of the distal at an angle of from 45 to 60 degrees, though in some cases the two planes are at nearly right angles with each other. In the present specimen the proximal end is turned outward much more than a right angle, perhaps 125 degrees, to such an extent, indeed, that

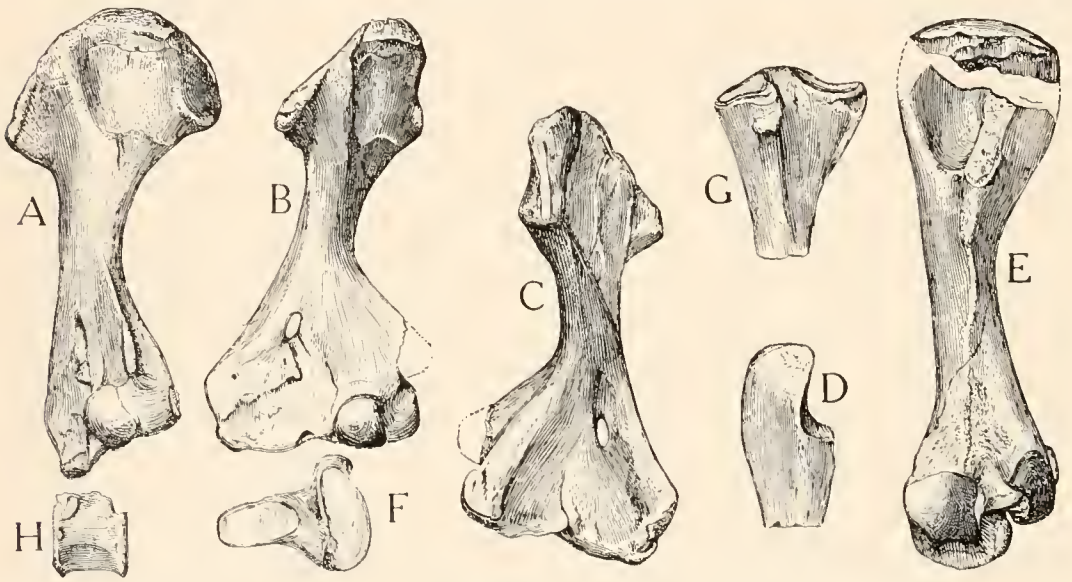

Fig. 37.—*Scoliomus puercensis*, × ½. A, left humerus, radial side; B, left humerus, ventral side; C, left humerus, dorsal side; D, left ulna, proximal end; E, left femur, ventral side; F, left tibia, proximal articular surface; G, left tibia, proximal end from in front; H, a dorsal centrum, left side.

the inner side of the proximal end is broadly visible from the dorsal side when the distal end is lying horizontal, whereas in all other humeri known to us from the Permo-Carboniferous the inner side is always more or less visible in this position. The entepicondylar foramen is large; it is situated rather low down on the bone, and is separated by a heavy bar from the inner margin. The femur is unusually slender. It differs from the femora of other known Permo-Carboniferous reptiles in the broad separation of the articular faces for tibia and fibula. The specimen is doubtless somewhat depressed, notwithstanding which the projection of the dorsal part beyond the articular surface for the fibula is unusual, and seems to indicate that, in natural articulation, the leg must have been constantly and considerably flexed upon the thigh. The upper end of the tibia shows the same broad separation of the articular facets for the leg bones. The trochanter is, for the most part, unfortunately wanting in the specimen. The linea aspera is distinguishable as a slightly rugose line, and is not at all prominent.

The single centrum preserved has an unusual character in the distinct but small parapophysial facet near its front margin. The diapophysis is not prominent. The centrum is sharply keeled below.

CHAPTER VI.

A DESCRIPTION OF CERTAIN COLLECTIONS OF BONES REFERRED TO SPHENACODON MARSH.

By E. C. Case and S. W. Williston.

Sphenacodon ferox Marsh.

Marsh, Am. Jnl. Sc., vol. xv, 1878, p. 410.
Baur and Case, Trans. Am. Phil. Soc., vol. xx, 1894, p. 4.
Case, Publication No. 55, Carn. Inst. Wash., 1907, p. 67.
Williston, American Permian Vertebrates, 1911, p. 78.

Marsh's original description of this genus is as follows:

"In the present genus the anterior teeth are somewhat like those of the reptile described above, but the posterior, or more characteristic ones, are totally different. The crowns are much compressed, and have very sharp cutting edges without crenulations. In the present species the carnivorous teeth are crowded together, and the crowns placed slightly oblique, and twisted. The jaws were comparatively short and massive. The rami of the lower jaws were apparently united by cartilage only, and the symphysis was short. The vertebræ are deeply biconcave.

"Measurements from the type of this species are as follows:

"Length of the dentary bone	150 mm.
Space occupied by the teeth	130
Extent of four anterior caniniform teeth	25
Extent of twenty compressed teeth	105
Height above jaw of second lower tooth	15
Depth of dentary bone at symphysis	26
Height of crown of compressed tooth	8
Transverse diameter	4

"This reptile was about 6 feet in length, and carnivorous in habit. Its remains are from the same locality in New Mexico that yielded those of *Nothodon*."

Marsh made no attempt to classify this animal further than to remark on its carnivorous habits. Baur and Case regarded it as belonging to the Clepsydropsidæ, and Case compared it directly with *Dimetrodon*. These conclusions were drawn from the imperfect lower jaw which forms the holotype of the genus and species. Williston assembled much more material in the Yale collection, and associated several bones which he regarded as doubtfully belonging with the genus; he also was unable to distinguish the genus positively from *Dimetrodon*. The collections made by the expedition to New Mexico in the summer of 1911 added much new material, but more decisive information as to the characters of the genus has been obtained from the Yale collections, which have been further worked out since the time of Williston's studies in 1910, and which have been attentively studied by him the present season. The material obtained by the Chicago-Michigan expedition may be described as follows:

This material consists of three lots of bones found in close association, together with numerous isolated bones, all from the banks of Poleo Creek in Rio Arriba County, New Mexico. The associated lots are:

First, ten dorsal vertebræ, eight of which are matrically connected, five of them with spines; and a separate coracoid. From the Miller quarry.

Second, an imperfect skull, including a nearly complete lower right ramus, lacking only the articular region; the anterior part of the left ramus, almost identical with the fragmentary holotype; the imperfect right maxilla with part of the nasals; a less perfect left maxilla; the external process of both pterygoids; both postorbitals; the lower border of the left orbit; a complete left quadrate; and a fragment of the right quadrate. With this skull were closely associated many other bones, including two complete vertebræ, three less complete, two clavicles, and a femur. From the Miller quarry.

Third, a poorly preserved skeleton, of which two dorsal vertebræ, part of the right maxilla, and a fragment of the scapula have been cleaned. This specimen was found isolated, embedded in a soft gray sandstone.

Other bones regarded by us as belonging to this genus are two scapula-coracoids, an imperfect pelvis, an axis, atlantal intercentrum, and three imperfect maxillæ, all from the Miller quarry.

Skull: It is not surprising that Case, in his first description of this genus, referred it to *Dimetrodon*, since, with all the fragments of the skull before us, representing a goodly portion of its structure, we are unable to discover a single character that would separate the form generically from that genus. It is practically only in the vertebræ that a distinction is possible. Williston has pointed out that the number of teeth in *Sphenacodon* is less than in *Dimetrodon;* he counted twenty-four in the holotype mandible; in the right mandible before us there are twenty-two, and, allowing for the presence of one anterior to the enlarged teeth and one at the posterior end, there would be exactly twenty-four. In the left mandible, making allowance for four which had been broken away from the upper margin, and for one in front of the enlarged tooth, and one at the posterior end, there are also twenty-four. The maxillæ are all imperfect, but they certainly had less than twenty teeth each. Williston counted sixteen in a maxilla associated with the holotype mandible. In the specimens before us the largest number is fourteen, with a possible maximum of three more, making seventeen. Case, from a study of numerous specimens of *Dimetrodon*, concluded that the number could not have been far from twenty-eight in the mandible and twenty in the maxilla. None of the teeth, as mentioned by Williston, are crenulate. In one specimen the bases of the large teeth are quadrangular in outline, as described by Case for *Theropleura*. The upper margin of the diastemal notch, anterior to the enlarged maxillary tooth, is nearly on a line with the alveolar border of the maxilla; that is, it does not ascend as in the more specialized members of *Dimetrodon* (e.g., *D. gigas*). In other characters, so far as the material we have studied goes, the skull of *Sphenacodon* can not be distinguished from that of *Dimetrodon*, and certainly none of these characters can be considered of generic value.

The *premaxillæ* in two specimens show but two large teeth in each, the anterior one much larger than the second. Williston has figured a specimen from the Yale collection with a third, posterior tooth, much smaller than the others.

The *maxilla* (fig. 38) has two enlarged teeth, which seemingly alternated in function, as in one of them the anterior tooth is the larger and the following one shows evidence of incomplete development. In another specimen the second tooth is the larger. This seems to bear out the conclusion expressed by Case that the large teeth in *Dimetrodon* alternated in function—that a single one performed the main work while the other was maturing, although in many specimens the two teeth are of nearly equal size. In the skull under description there are no teeth in the notch anterior to the enlarged tooth, but in other specimens in the collection, and also in a specimen in the Yale collection, as figured by Williston, there are two small teeth.

The *nasals* are too incomplete to describe fully. They were narrow and seem to closely resemble the same bones in *Dimetrodon*, indicating that, as in that genus, the skull was narrow and high in the facial region. The cast of the top of a skull observed in a large boulder in the field shows the same character.

The *mandible* (fig. 39 A) of the right side is complete, with the exception of the articular region. It resembles very closely the jaw of *Dimetrodon*. The only difference noticeable is the sharp upward bend of the anterior end, causing the anterior teeth to point backward at a considerable angle with the axis of the jaw. This is, in part at least, due to distortion of the right mandible, since the ramus

FIG. 38.—*Sphenacodon ferox* Marsh, × ½. A, right maxillary, imperfect; B, inner surface of fragment of second right maxillary.

of the left side does not show this character to anywhere near the same extent. The sutures, so far as they can be made out, are identical with those of the *Dimetrodon* mandible.

The *pterygoids* are represented by the external processes only; they are indistinguishable from the same processes in *Dimetrodon*. A single row of medium-sized, conical teeth is found on the lower margin.

The lower rim of the orbit, formed by the maxilla and jugal, the postorbital bones of the two sides, and the quadrate are indistinguishable from the same bones in *Dimetrodon*.

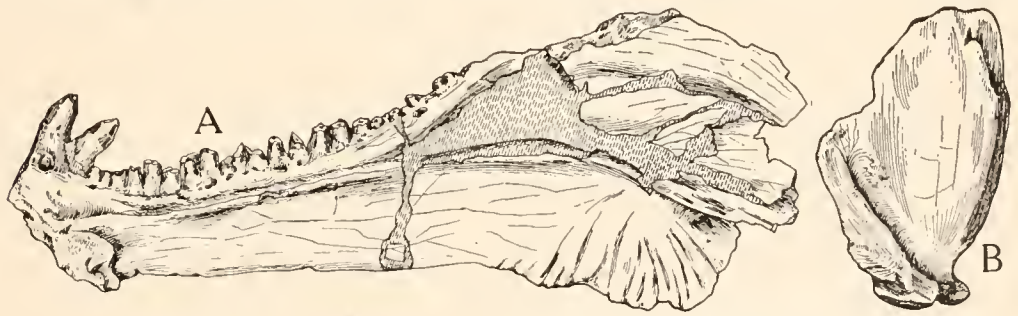

FIG. 39.—*Sphenacodon ferox* Marsh, × ½. A, inner surface of a right ramus; B, quadrate.

There can be no doubt of the great resemblance of the skull of *Sphenacodon* and *Dimetrodon*—so great a resemblance that, on the strength of this part only, we would not be justified in considering the genera distinct.

Three imperfect *scapulæ* are preserved in the collection. One, associated with a considerable part of the skeleton in a bad state of preservation, is known only from a fragment of the blade. Another, an isolated specimen, lacks the anterior edge and has the two proximal bones attached (fig. 40 A). The third, also an isolated specimen, lacks the anterior border and the border of the coracoids. As a whole the shoulder blade is quite similar to that of *Dimetrodon*. The sutures between

the scapula and coracoid (metacoracoid Williston) and procoracoid (coracoid Williston) are distinct, and the posterior bone is easily separable—there are two isolated posterior coracoid bones in the collection. The anterior border of the bone is destroyed in both specimens, so that it is impossible to determine the presence or absence of facets for the attachment of a clavicle or cleithrum. The proximal end carries a large preglenoid tuberosity, with an articular glenoid face looking backward and downward. There is no foramen on the posterior face of the preglenoid tuberosity, such as occurs in *Dimetrodon*. Below the posterior part of the edge of the tuberosity there is an indication of a glenoid foramen, and below the anterior part of the same border is the usual supracoracoid foramen. Both foramina open into a subscapular fossa on the inner side of the bone, as in *Dimetrodon*. The posterior of the two coracoid bones has the same form as in *Dimetrodon*. The glenoid face looks

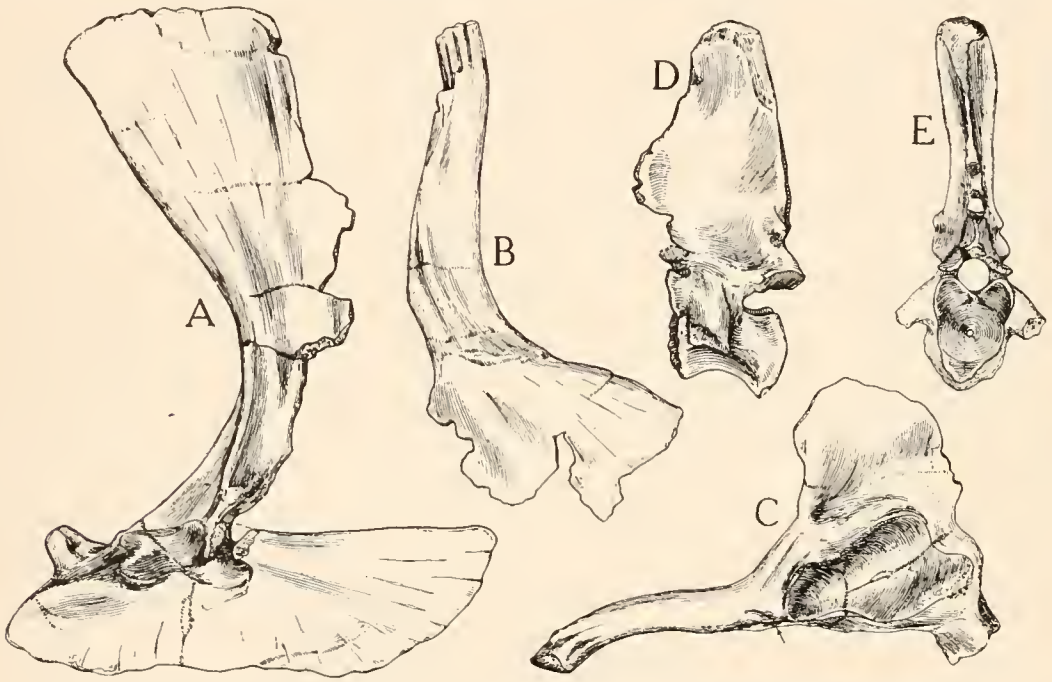

FIG. 40.—*Sphenacodon ferox* Marsh, × ½. A, right scapula; B, left clavicle; C, fragment of left side of pelvis; D, left side of axis; E, anterior view of axis.

forward, upward, and outward, completing the glenoid cavity identical in form and position with that of *Dimetrodon* and *Ophiacodon*. The anterior coracoid bone, the procoracoid of authors, is complete in one specimen, but the scapula is broken away along the line of union between the two (fig. 40 A). This edge is perfect, extending almost directly outward from the lower part of the scapula. As a whole, the proximal margin formed by the two coracoid bones is nearly straight, except at the front end.

Clavicles (fig. 40 B): Associated with the skull are two clavicles. That of the right side is more perfect than that of the left; its proximal end is wide and flat, and evidently articulated with the interclavicle, as in *Dimetrodon*. The distal end is narrower, and there is a deep groove on the lower edge which received the border of the scapula. The anterior border is deeply concave longitudinally. The whole bone is different from that of *Dimetrodon;* in that genus the proximal end is wider and the distal end narrower, without a groove on the lower edge for the scapula.

Pelvis (fig. 40 c): The pelvis is represented by a portion of the left half, showing the cotylus and the outer part of the pubis. A much better specimen of the Yale collections is shown in fig. 43 D.

The *cotylus* is rather narrow and deep, with prominent edges on all of the bones; in this it differs from *Dimetrodon*, in which the edge of the cotylus on the pubis is not elevated. This permitted the femur of *Dimetrodon* to be extended much more directly forward than in *Sphenacodon*, in which it must have stood almost directly out from the side of the pelvis. The ilium is too incomplete for any detailed description; the crest was broad, differing notably from that of *Theropleura*, which is narrow, resembling the ilium of *Varanosaurus*. That it was firmly attached to the sacrum is shown by the prominent rugosities on the inner side. In *Dimetrodon* there is a narrow process on the proximal edge of the ilium, which forms a buttress against which the end of the femur fitted; in *Sphenacodon* the whole edge is elevated, though there is a narrow portion on the posterior part which carries the face for the femur. The outer edge of the pubis is thickened; it runs directly forward from the cotylus and is slightly deflected at the distal end. The opening of the pelvis was rounder than in *Dimetrodon*, in which it was distinctly angular at the lower part. The pubic foramen perforates the bone at a point just below and anterior to the cotylus.

The *vertebral column* is represented by an atlantal intercentrum, an axis, several vertebræ associated with the skull, and ten others closely associated together. The intercentrum is broad below and of good size. Its anterior face is deeply concave, both vertically and horizontally, indicating a well-rounded condyle. Its posterior face is smaller and more shallow; the posterior edge of the lower surface has a shallow notch in the middle. The presence of atlantal ribs is indicated by small facets on the upper part of the posterior margin. The axis resembles that of *Dimetrodon* much more closely than that of *Ophiacodon* or *Theropleura*. In the latter the spine is short and the distal end is fully as long, anteroposteriorly, as the rest of the spine; the anterior and posterior margins are nearly vertical, with no projection of the lower part of the anterior end forward over the atlas. The axis of *Sphenacodon* (fig. 40 D, E) has an elevated neural spine, the lower part of which extends forward, terminating in a slight rugosity, beyond which the border slopes upward and backward slightly concave in outline to the rather wide and triangular apex.

The posterior border of the spine is nearly vertical and for its lower two-thirds deeply excavated by a narrow groove, which increases in depth downward until it reaches its maximum at the level of the posterior zygapophyses. The edges of this groove are sharp, and there is a small but prominent knob or process just over each posterior zygapophysis. We have never seen such a process on the axis of *Dimetrodon* or other pelycosaur. The anterior zygapophyses are small, but well formed; they look almost directly upward and but slightly outward. The posterior zygapophyses are relatively large for the size of the axis. The anterior face of the centrum is elongate and heart-shaped, due to the development of a sharp keel on the lower surface. On the upper edge of the articular face there are two large, elliptical, concave faces, centantra, looking slightly inward and downward; they are relatively much larger than any observed in *Dimetrodon*. The posterior face of the centrum is circular, with no faces on the upper margin corresponding to those of the anterior face.

Centantra and centrosphenes do not seem to occur on the post-axial vertebræ. The sides of the centra are deeply concave and terminate below in a sharp keel, which has a very sharp line on its lower surface. The keel and concavities of the

sides terminate before the anterior and posterior borders are reached, due to the wide flaring out of the edges; this flaring is especially prominent in the posterior face. The transverse process rises from the neural arch and the upper part of the centrum, and extends outward, backward, and downward, as in *Dimetrodon*. The axis is decidedly like that of *Dimetrodon*, differing only in the tuberosities over the posterior zygapophyses, the large size of the latter, and the size of the centantra above the anterior articular face. (Compare figs. 32–35 and 58, 59, Publication 55, Carn. Inst. Washington.)

The ten dorsal vertebræ, eight in connection (fig. 41 A), are from the middle or posterior part of the series; they all have short, smooth spines, somewhat flattened, and with the anterior-posterior diameter the longer. The base is narrowed and somewhat recurved, above which the spine expands gradually to the upper end and terminates in a flat face. They are easily distinguishable from the vertebræ of *Ophiacodon*, in which the spines are less dilated and thickened above. We observe no rugosity on the sides of the spines just above the base, such as occurs in

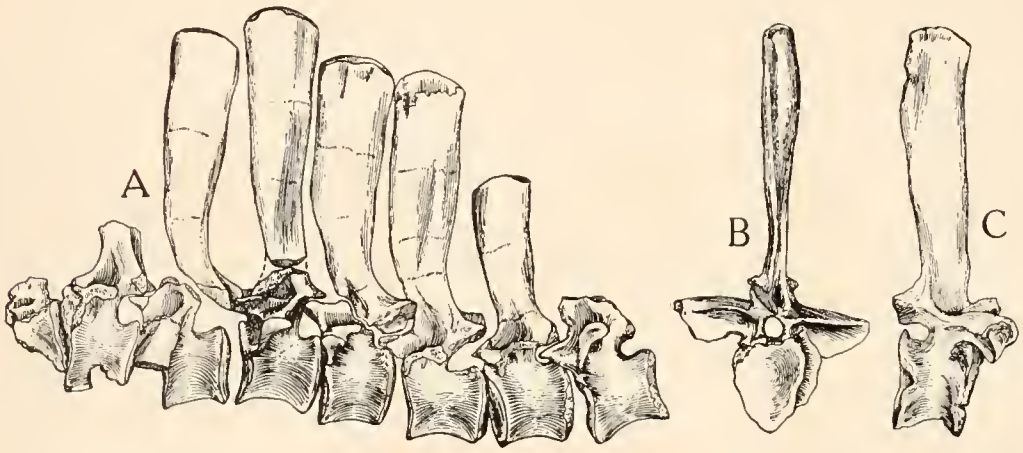

FIG. 41.—*Sphenacodon ferox* Marsh, × ½. A, dorsal vertebræ; B, anterior view of a dorsal vertebra; C, lateral view of same vertebra shown in fig. B.

Dimetrodon, and which doubtless marks the attachment of the dorsal muscles and the beginning of the thin cutaneous covering of the spines. The spines are relatively much higher than in *Ophiacodon* or *Theropleura*. That there was some variation in the height of the spines is indicated by the fact that of the five vertebræ with spines attached, one, the last, has its spine notably shorter than the others.

The short transverse processes rise from the base of the neural arch and extend directly outward; the upper side of the process is thickened and convex; the lower is very narrow and does not pass obliquely downward to join the anterior border of the centrum, but is set off from it sharply, indicating dichocephalic ribs. As there is no face for the rib on the anterior edge of the centrum in these specimens, nor any on the ends of the single dorsal intercentrum preserved, it seems probable that the capitulum articulated, as usual, with the intercentral cartilage. The sides of the centra are concave and there is a sharp median keel. The articular faces are elongate, and, due to the presence of the keel, narrowed below.

Two vertebræ (fig. 41 B, C), probably from the anterior dorsal region, have much higher spines and even more prominent transverse processes than those of the series of ten. These stand out almost directly from the sides of the neural

arch, with the broad upper surface on a level with the anterior zygapophyses. It is evident that these vertebræ closely resemble those of *Dimetrodon*, especially the form described as *D. giganhomogenes* by Case, but the faces of the centra are relatively more elongate and the longer transverse processes do not dip so far downward, as is common in all species of *Dimetrodon*. As compared with *Theropleura*, which *Sphenacodon* resembles in some respects, the centra are much narrower below and the sides are concave, the faces of the anterior dorsal vertebræ are more elongate, and the spines are higher and narrower.

It is apparent that *Sphenacodon* was closely related to *Dimetrodon*. The skull is, so far as can be determined from known material, almost identical; the few resemblances to *Theropleura* which have been pointed out are all of a primitive character. We regard *Sphenacodon* as a less specialized member of the group of dimetrodonts, which had not yet acquired those habits, whatever they were, which led to the excessive development of the spines and the more elongate and slender limbs. The position of the femur, directed nearly straight outward, indicates a more sprawling habit of body. Perhaps the animal had not yet so thoroughly adapted itself to the dry-land habitat which seems to be characteristic of the specialized, long-spined forms.

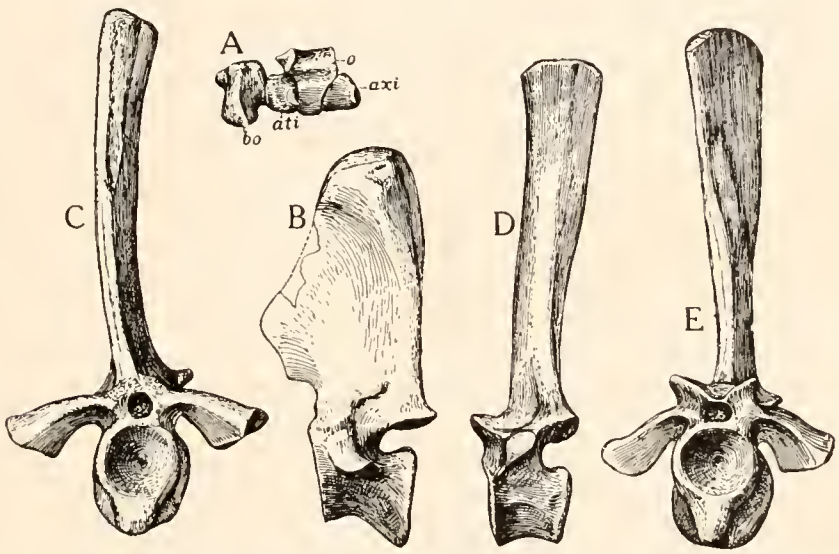

FIG. 42.—*Sphenacodon ferox* Marsh, No. 818, Yale University, × ⅜. A, basioccipital, intercentra, and odontoid seen from the side; B, left side of an axis; C, anterior view of a posterior cervical vertebra; D, lateral view of a dorsal vertebra; E, anterior view of a posterior cervical vertebra.

NOTE BY WILLISTON.—The foregoing material collected by us in New Mexico is of great interest, but leaves in doubt several important problems as to the relationships and structure of this genus; this doubt is partly, not entirely, dissipated by the better collections of the Yale Museum, made by Baldwin so long ago. Williston had the privilege of studying this material, though not as fully as he desired, the past summer. Several specimens, which must be referred to the genus *Sphenacodon*, have been thoroughly prepared, and settle beyond dispute the general characters of the genus, though it is by no means certain that they all belong to the same species as that originally named by Marsh from material from the Baldwin quarry. The most important and best preserved of these specimens is No. 818 in the Yale collections, coming from the "Rito Puerco." It was embedded in a red sandstone, and the bones are somewhat crushed, and many fragments are missing. It includes the two innominata, scapula, humerus, part of skull, axis, about twenty verte-

bræ, apparently in a connected series, a few caudal vertebræ, and an incomplete femur. Figures of many of these bones, carefully made by Williston, are given in figs. 42–45 and will render an extended description unnecessary. The vertebral spines, it will be seen, are all of nearly uniform length, though they shorten somewhat toward the axis; they are dilated and thickened above, rounded and stout below. On a number of the posterior ones (fig. 43 A, B, C) there is a facet, it will be observed, for the capitulum, an unusual thing in the Pelycosauria. The axis agrees with the specimen previously described. The nearly complete innominate bone (fig. 43 D) is indistinguishable from that of *Dimetrodon*. The scapula (fig. 44 A) shows only minor differences in comparison with an unusually well-preserved scapula of *Dimetrodon*, collected by Mr. Hatcher on Coffee Creek, Texas, and preserved among the Yale collections (fig. 44 B). The sutural lines between the scapula and coracoids are shown very clearly in both specimens. In the specimen of *Sphenacodon* the preglenoid facet is imperfect. The humerus (fig. 45 A) also shows an amazing resem-

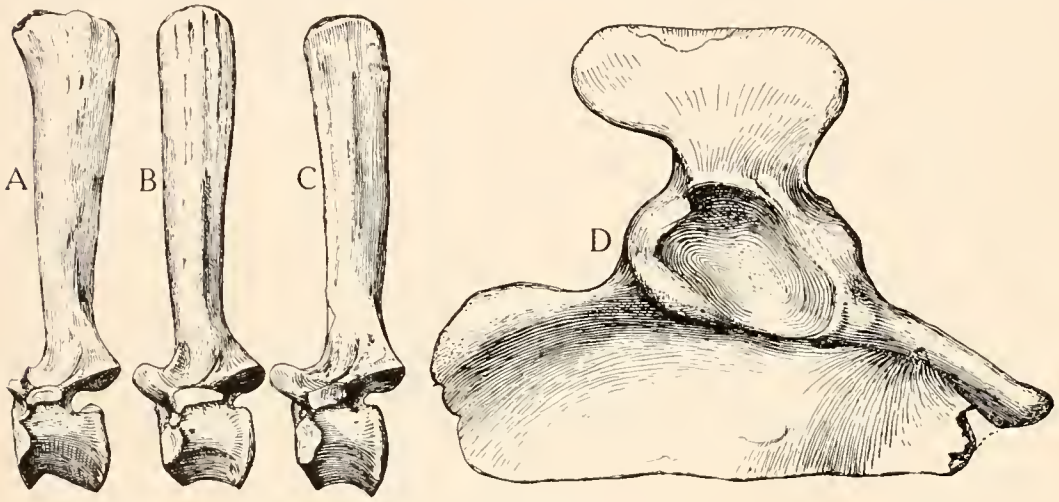

FIG. 43.—*Sphenacodon ferox* Marsh, No. 818, Yale University, × ⅔. A, B, C, lateral view of three posterior dorsal vertebræ; D, right innominate bone.

blance to that of *Dimetrodon*.* The femur of this specimen is imperfect; a perfect femur from another specimen, agreeing well with this incomplete one, except that it is slightly smaller, is shown in fig. 45 B.

The sacrum is quite that of *Dimetrodon*, so far as the incomplete specimens show; it has three vertebræ. The parts of the skull of this and other specimens in the Yale collection indistinguishable from it agree very well with the ones referred to the type specimen, except in size.

As has been stated, there seem to be minor differences in the length and characters of the spines among the material in the Yale and Chicago collections that might indicate specific variations. Possibly, when the complete anatomy of the genus is known, as in *Ophiacodon*, these differences may justify its separation into two or more closely allied genera. The size, typically, is smaller, and no such broad-ended spines as those figured herewith as belonging with specimen No. 818 of the Yale collection have been discovered in the Baldwin quarry, whence came the holotype specimen of Marsh; though on the other hand, this collection does contain spines too long for *Ophiacodon*, though thinned above. But these details are unimportant at the present time. The one thing now absolutely

* It was chiefly on this humerus, together with the incompletely prepared spines of this specimen, that I reported in an earlier paper the occurrence of *Dimetrodon* in the New Mexican fauna. As a fact, there is not a single specimen in either collection which can now be referred with any probability to the genus *Dimetrodon*. I think it may be definitely said that the genus does not occur in New Mexico.

determined is that *Sphenacodon* is a typical pelycosaur, very closely allied to *Dimetrodon*, with only minor differences in skull, girdles, extremities, and vertebral centra, but with very much shorter spines, which are not pointed at their extremities, but, on the other hand, are dilated antero-posteriorly. The spines are long, extraordinarily long for a reptile, but they could not have formed any such frill as that of *Dimetrodon* or the basilisk lizard.

And this structure of the vertebra has an important bearing in any discussion as to the meaning of the spines in *Dimetrodon*. That *Dimetrodon* could have developed such extraordinary spines without affecting to a greater degree the characters of the skeleton proves conclusively their relative physiological unimportance.* Certainly, had the enormous dorsal expansion of *Dimetrodon* been of profound importance in the life economy of these

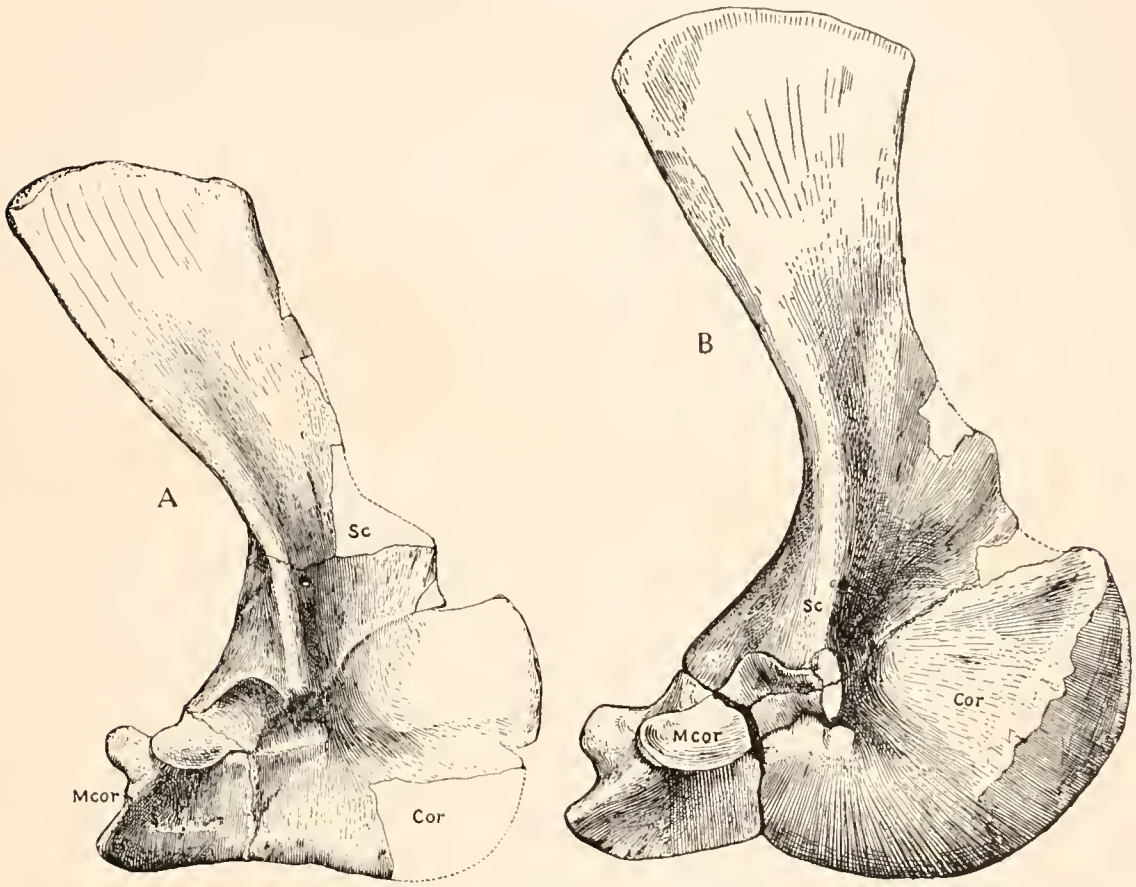

FIG. 44.—*Sphenacodon ferox* Marsh. A, right scapula, No. 818, Yale University, × ⅓; B, right scapula of a large *Dimetrodon* from Coffee Creek, Wilbarger County, Texas, No. 661, Yale University, × ⅓.

creatures, it must have materially affected the structure of the skeleton elsewhere. That *Sphenacodon* is more primitive than *Dimetrodon* must be admitted to be perhaps another bit of evidence of the greater antiquity of the New Mexico deposits than the upper ones, at least, of Texas.

*Case would hesitate to indorse the statement that these elongated spines were physiologically unimportant. He has long considered (and frequently stated his belief) that the enormous development of the spines in *Dimetrodon* and probably also in *Edaphosaurus* (*Naosaurus*), imposed upon the creatures a physiological burden so great in its demands upon the energies of the individual, both for their original production and the repair of frequent injuries, that it was an important, if not the chief, cause of their extinction.

With differences that can hardly be accounted of generic value elsewhere in the skeleton, it would be idle to claim for the greater spinous expansion of *Dimetrodon* a family value in their classification. Whence it follows that in the strict application of the laws of priority, the family name *Sphenacodontidæ* (Marsh, May 3, 1878) must take precedence over *Clepsydropidæ* (Cope, May 8, 1878), provided no question of scientific rectitude on the part of its author is raised.

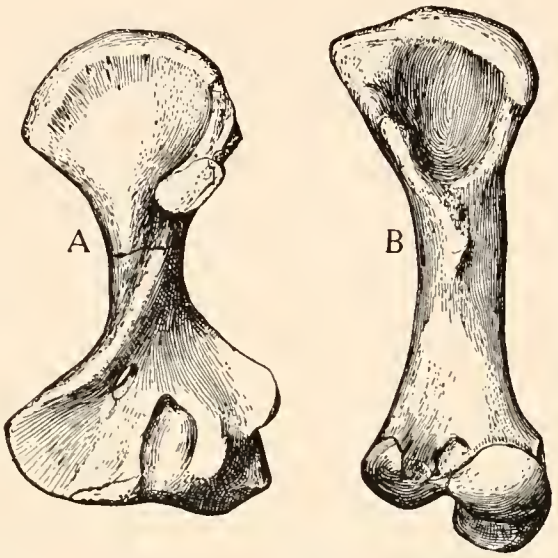

FIG. 45.—*Sphenacodon ferox* Marsh, × ⅜. A, ventral surface of a right humerus, No. 818, Yale University; B, ventral surface of right femur, × ⅜.

CHAPTER VII.

A DESCRIPTION OF EDAPHOSAURUS COPE.

By S. W. Williston and E. C. Case.

The detailed history of the genus *Edaphosaurus* has been given by Case * and need not be repeated here. Briefly, the genus was described by Cope in 1882, based upon a fairly complete but crushed skull and a single vertebra, the axis. The characters presented by this specimen were deemed of sufficient importance by Cope to warrant the erection of the family Edaphosauridæ, in which, however, he erroneously associated the cotylosaurian genus *Pantylus* Cope, a genus having somewhat similar palatal teeth, but differing widely in other respects. In 1884 he referred a second species, *E. microdus* Cope, to the same genus, based upon some fragments of the plates bearing the teeth and a series of vertebræ. Two years later, however, Cope transferred the latter species to his new genus *Naosaurus*, where it has since remained.

Until recently no additional specimens have been referred with certainty to *Edaphosaurus*, and the identity of the two genera, *Edaphosaurus* and *Naosaurus*, has been in doubt. Six years ago, however, Case discovered in the Texas deposits typical *Naosaurus* vertebræ associated with a mandibular dental plate, which pretty nearly convinced him of the identity of the two genera, as shown by the following quotation from his cited work, page 45:

"If this association is a true one, as seems certain, the name *Naosaurus* must be given up, as it is preoccupied by *Edaphosaurus*, and the subfamily Naosaurinæ will disappear, and the members will be placed in the family Edaphosauridæ. It may seem that there is undue hesitancy in uniting the two genera on the evidence cited, but to any one familiar with the occurrence of bones in the Texas beds the possibility of accidental association is so evident that the greatest conservatism seems the best course. * * * To me it seems extremely probable that the two genera must be united."

As will be seen, Case was quite right in his opinion; the evidence is now positive that the two genera are closely allied if not identical, and the name *Naosaurus* must be abandoned, unless it should be found that the typical species *N. claviger* Cope is generically different from *Edaphosaurus* in ways that are yet unknown. That the genus belongs in the family Edaphosauridæ is, in any event, definitely proven. In some ways it is unfortunate that the identity or close relationship of the two genera was not more strongly insisted upon by Case; it might, perhaps, have prevented the incorrect restorations of *Naosaurus* which have gained currency in textbooks and popular works. The following, to the best of our present knowledge, is the correct synonymy of the genus and species:

EDAPHOSAURIDÆ.

Cope, Proc. Amer. Phil. Soc., xx, 1882, p. 450; ibid, 1883, p. 631; Pal. Bulls. 35, 36. Case, Revision of the Pelycosauria, 1907, 68.

Edaphosaurus.

Cope, Proc. Amer. Phil. Soc., xx, 1882, p. 448. Case, Revision of the Pelycosauria, 1907, p. 69. *Naosaurus* Cope, Amer. Nat. xx, 1886, p. 544; ibid. xxi, 1878, p. 319; Proc. Amer. Phil. Soc. xiv, 1878, 44 (*Dimetrodon*). Case, Revision of the Pelycosauria, 1907, p. 58.

* Revision of the Pelycosauria, Carn. Inst. Washington, Publication 55, 1907, p. 34.

EDAPHOSAURUS—Continued.

Edaphosaurus pogonias Cope, Proc. Amer. Phil. Soc., XX, 1882, p. 448; Trans. Amer. Phil. Soc., XVII, 1892, p. 15, pl. xi, ff. 5, 5*a*. Case, op. cit., 1907, pp. 69, 151, pl. xxxiv.

Edaphosaurus microdus Cope, Proc. Amer. Phil. Soc., XXII, 1884, p. 37.

Naosaurus microdus Cope, Amer. Nat., XX, 1886, p. 544; Trans. Amer. Phil. Soc., XVI, pp. 287, 295. Case, op. cit., 1907, p. 61.

Edaphosaurus claviger Cope.

Naosaurus claviger Cope, Amer. Nat., XX, 1886, p. 544; Trans. Amer. Phil. Soc., XVI, 1888, pp. 287, 293, pls. ii, iii. Case, op. cit. pp. 59, 139, pls. xxviii, xxix, xxx, 1907.

Edaphosaurus cruciger Cope.

Dimetrodon cruciger Cope, Amer. Nat., XXI, 1878, p. 829; Proc. Amer. Phil. Soc., XIX, 1880, p. 44.

Naosaurus cruciger Cope, Amer. Nat., XX, 1886, p. 544; Case, op. cit., 1907, pp. 60, 146.

Edaphosaurus novomexicanus Williston and Case, infra.

Until the material described in the present paper was discovered, the type specimen of *Edaphosaurus pogonias* preserved in the American Museum was the only one of the genus confidently known. This specimen, unfortunately, was so crushed in fossilization that its true characters were very difficult to determine; attempts to restore it by Case and Broom were only in part successful, as will be seen.

In the summer of 1910, Mr. Paul Miller was so fortunate as to discover, on Moonshine Creek, in Baylor County, Texas, probably from the lower Clear Fork

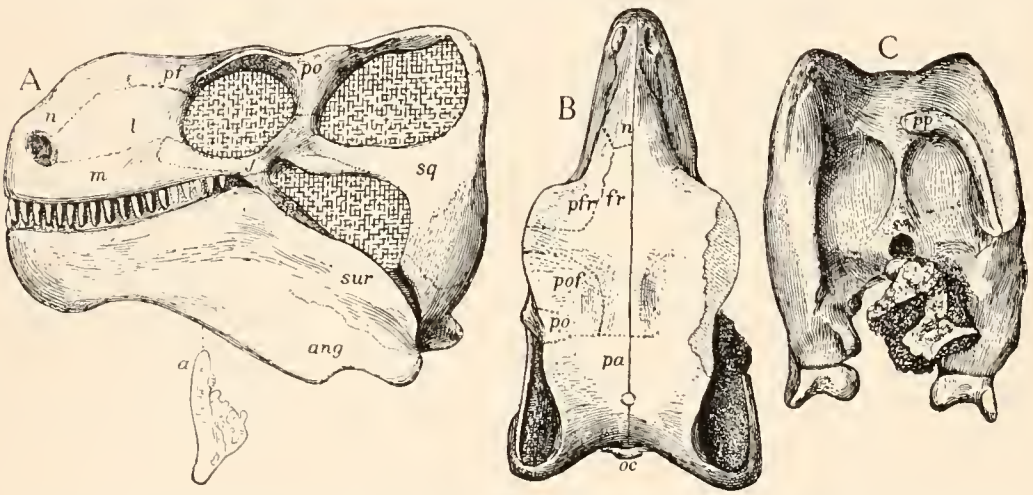

FIG. 46.—Skull of *Edaphosaurus ? pogonias* (Cope) Williston and Case. No. 625, University of Chicago, × ⅔. A, from the left side, *a*, section of the jaw; B, from above; C, from behind. *ang*, angular; *fr*, frontal; *l*, lachrymal; *m*, maxilla; *n*, nasal; *pa*, parietal; *pfr*, prefrontal; *pof*, postfrontal; *pt*, pterygoid; *sq*, squamosal; *sur*, surangular; *po*, postorbital; *oc*, occipital condyle.

beds, an excellent skull referable with certainty to *Edaphosaurus*, but whose precise specific determination is impossible at the present time. From *E. pogonias* it seems specifically different in the proportions and shape of the bones of the upper side, and, as the skull is quite unknown in the other described species, it may be a long while before its specific identity is certainly proven. In much probability some one or another of the three species, *E. claviger*, *E. cruciger*, and *E. microdus*, is identical with *E. pogonias*, and the giving of a new specific name to the present specimen, while temporarily convenient, would in the end probably encumber the synonymy to a still greater extent. This species, until more is known of the allied ones, may be known as *E. ? pogonias* Williston and Case. Comparisons of the specimen will be made in the discussion of the following species, *E. novomexicanus*, the skull of which seems more nearly like that of the type.

The *skull* (fig. 46) as a whole is very high, narrow, and short, subquadrilateral in shape, less deep in front, with the nasal region convex. Its greatest width above

is between the orbits, due to the projecting, overhanging, and somewhat upwardly curved roof of the orbits, which is convex on its margin and thinned. The parietal region is narrower, but certainly less narrow than in the genotype specimen, and is concave transversely. The parietal foramen is situated rather far back. In front of the orbits the skull rapidly narrows triangularly, nose-like, and is convex in outline, terminating in a thin, median, prominent ridge, which descends convexly between the closely approximated nares. The side of the skull is conspicuous for the large, oval, single temporal vacuity, lying immediately back of the orbit, but higher posteriorly, and narrowed in front. It has the thickened lateral margin of the parietal above, the thickened and short postorbital bar in front, the convex border of the parietal arch behind, and a rather slender temporal bar below. The quadrate, covered by a temporal bone, descends far below the arcade posteriorly, leaving a large open space in the articulated skull between the temporal bar and the upper margin of the mandible. If any quadratojugal bone is present in the arcade it must occupy an anomalous position. There is but a single temporal arch and a single temporal opening, in the formation of which it is quite evident the squamosal bone must participate, and into which it seems quite as evident that the quadratojugal does not enter. If this vacuity be, as is urged by Huene and Broom, the lateral temporal vacuity, and not the upper one, the relations of the bones have become sadly mixed. In all probability the temporal bar is formed exclusively by the squamosal and jugal, and it is also not at all improbable that the squamosal reaches toward, if it does not actually join with, the postorbital. By this we do not mean to say that we believe the opening is the upper vacuity, but simply that the attempt at present to differentiate the upper and lateral vacuities in the reptilian single-arched skull is premature and unreliable.

The orbit is subrotund in shape, a little longer in the oblique diameter from above downward anteriorly. Its roof is very prominent, projecting horizontally and a little upward, its border gently convex. Below, it is separated by a short, slender bar from the vacuity above the mandible in the articulated skull. The face in front of the orbit is somewhat concave on its upper part. The external nares are small, round in shape, situated close to the front margin at a considerable distance above the alveolar margin.

Posteriorly the skull is deeply concave between the parietal projections. On either side there is a concavity above the stout suspensorium, which articulates with the quadrate a little above the level of the temporal arch. Doubtless there is a post-temporal vacuity between the parietal bar and the paroccipital, but it can not be distinguished in the specimen. On the right side, lying back of the downwardly curved parietal process, and reaching inwardly to the middle line, there is a long, rather slender, and curved bone, which seems to be distinct. If so, it must correspond to that figured and described by Case as the "? epiotic" in the type specimen of the genus. Broom, however, doubted its presence. If the bone be really distinct, and it seems to be, it can hardly be the tabulare, inasmuch as we know of no vertebrate skull in which the tabularia meet in the middle line. Its relations seem to be more those of the postparietal; but even this interpretation is open to doubt.

The mandibles, as seen from the side, are very broad posteriorly. The tooth-border is nearly straight. From the rounded and not at all prominent coronoid angle the thin upper border descends obliquely to the articulation for the quadrate. In front, the two sides meet in a very firm symphysis, the front border of which is thinned and convex in outline, descending below the mandibular border back of it, where the mandible is the narrowest, its width not half that opposite the coronoid elevation.

The skull, while in most excellent preservation so far as its shape and absence of distortion or loss of parts are concerned, will not permit the determination of the sutures with any degree of certainty. Certain lines, by their symmetry on the two sides, seem in much probability to indicate sutures, but it is quite impossible for any one to say with certainty that they really do so without the corroboration of additional material. These lines are indicated by dots; those of the face and upper side seem very probable; the others are more doubtful (fig. 46).

Dentition: On the right side of the specimen the maxillary teeth are all, or nearly all, shown clearly; those of the mandibles are more obscure. There are four premaxillary teeth, if the division between the maxilla and premaxilla is where it is assumed to be, below the back part of the naris. Back of these four teeth there are definitely nine or ten on the maxilla in front of the orbit. These teeth are not nearly so broad at the base as they were figured by Case; they do not differ much in size, though the median ones are the longest and largest. Back of these teeth there are four or five, possibly more, extending at least as far as the middle of the orbit; they are of smaller size. Broom criticizes Case's interpretation of the maxillary teeth, but his own is no better; there are not nearly so many as he figures, and they extend much farther backward.

In the closely articulated position in which the mandibles are preserved in this specimen it was impossible to ascertain the most essential characteristic of the genus, the palatal and mandibular teeth. In order to determine their extent and position a section nearly 2 inches in length was smoothly sawed from the right mandible; and this section enables one to determine with certainty, not only the presence of such teeth as were described in the genotype, but also their position. In this section of the mandible as separated from the pterygopalatine, numerous round teeth are seen, as also those of the opposing surface, the two sets attached to their respective bones in a plane divergent from the vertical by about 45 degrees, as shown in the figure of the front end of the section (fig. 46 A, *a*). The palatine and splenial teeth have hitherto been supposed to be placed more nearly horizontal. On the outer side, the stout and rounded upper border of the dentigerous pterygoid plate is seen just above the coronoid, where it joins the jugal. From this junction the border is directed backward and downward for more than two-thirds the distance to the articulation of the quadrate with the mandible. The apparent fusion of the pterygoid with the jugal would suggest the presence of a transverse bone. So far as the teeth are visible in the section broken away from the pterygopalatine plate, they seem to be quite like those described in the following species. The narrow space between the mandibles below does not permit the preparation of the palatine region, especially so as posteriorly the region is more or less occluded by a fragment of the vertebral column.

Edaphosaurus novomexicanus, n. sp.

A somewhat crushed specimen, discovered by Dr. v. Huene in the vicinity of Arroyo de Agua, New Mexico, may be referred provisionally to a new species. Although somewhat fragmentary, the specimen is of importance as furnishing for the first time indubitable evidence of the relationship of *Edaphosaurus* and *Naosaurus*. The specimen consists of the skull and a connected series of fifteen vertebræ, together with the two incomplete scapulæ, the right clavicle and a part of the left one, the left cleithrum in articulation with the scapula, a number of ribs, a humerus, and a radius. Some of the vertebral spines had been weathered out of the matrix, and the pieces into which they were broken can not be reunited, because of the absence of many.

The skull is about as complete as the genotype, with the exception of the mandible, of which nothing has been detected. Like that specimen, it is crushed nearly flat. By careful labor the broken parts have all been reunited, and the whole has been carefully cleaned of its investing matrix; unfortunately some fragments were not recovered. The skull is shown in fig. 47, as carefully drawn by Williston. The upper side resembles in its proportions the original type better than it does that of the skull described on the preceding pages, especially so in the relative widths of the interorbital and interparietal regions.

On the palatal side the two large plates bearing the teeth are nearly complete, that of the right side quite so. About seventy-five teeth are visible on this side; possibly there are a few more. The teeth vary not a little in size. They are hemi-ellipsoidal in shape. The more newly erupted, smaller ones have the apex

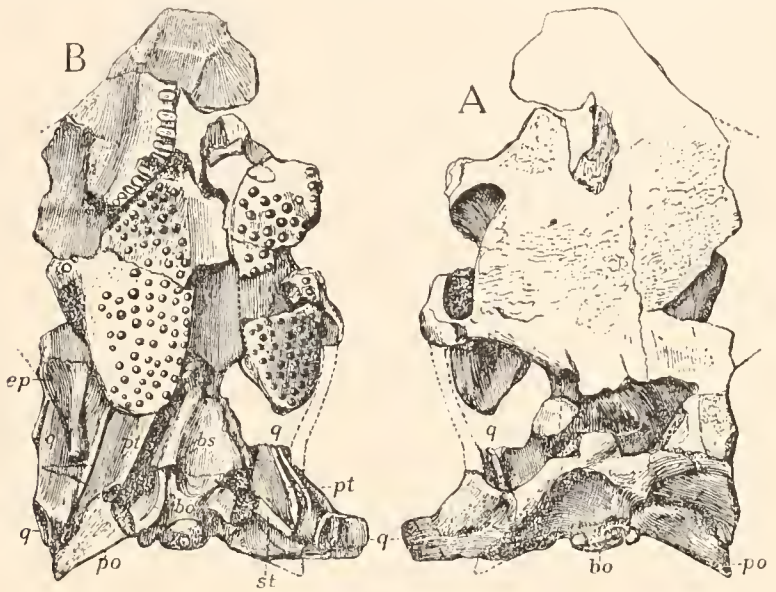

FIG. 47.—*Edaphosaurus novomexicanus* Williston and Case, × ½. A, skull from above; B, skull from below; *bo*, basioccipital; *bs*, basisphenoid; *ep*, epipterygoid; *po*, paroccipital; *pt*, pterygoid; *q*, quadrate.

somewhat pointed, but most of them are worn a little at the top. They are inserted in pits, thecodont, or protothecodont. The anterior part of the plate is angulated somewhat from the larger posterior part, about in the place where Broom thought the palato-pterygoid suture occurs; possibly the angulation indicates a suture, but that can not be determined. The maxillary teeth extend back to about the middle of the pterygo-palatine teeth, and beyond the middle of the orbit. There is no evidence of a posterior palatine vacuity; there is certainly none in the place figured by Broom in his restoration. The region in front of the middle is injured in the specimen, and its structure can not be made out; there are no vomerine teeth visible.

Posteriorly the basisphenoid has a deep median fossa, on either side of which, behind, there is a descending basisphenoid process; the distal end of the stapes is visible. The quadrates are visible in large part They are shaped much like those of the true pelycosaurs, consisting of a thin, expanded plate directed obliquely forward and inward, articulating on the outer side with the lower part of the squamosal or quadratojugal, on the inner side by a large and firm surface with the

posterior end of the pterygoid, the posterior lower edge of which extends to within 8 mm. of the condylar margin. The condyle is transverse, the inner side descending lower than the outer, with a trochlear groove in the middle. The posterior part of the pterygoid, beyond the dentigerous plate, is a thin, flat, or gently concave process, articulating at its extremity with the quadrate, as described. On the right side, lying on the outer side of the quadrate expansion, which is here exposed, there is a smooth rod, expanded above, where it lies in juxtaposition with the parietal; more slender below, its lower end doubtless dislodged from its original position above the dentigerous plate. It must be the epipterygoid.

The occipital condyle is gently convex, subcordate in outline, with the usual notochordal pit in the middle. On either side of the foramen magnum there is a projection having, apparently, an articular facet, doubtless for articulation with a proatlas. On the side of the skull there was a slender temporal bar like that of the skull described in the preceding pages, the most of which was broken away and the pieces lost. Its free, thin border curves downward posteriorly to very near the condylar margin of the quadrate, with which the bone articulates. Broom's conjectural restoration here is incorrect; the free border of what he supposed was a foramen in the arch is merely the lower border of the temporal arch; and there are no indications on the smooth surface here of a suture distinguishing a quadratojugal.

From the two specimens of skull figured herewith it will be seen that the conjectural restorations of *Edaphosaurus* were both incorrect; in some details that of Case is the better, in others that of Broom. The orbit is not as large as Broom figures it; the quadrate descends much lower; the single temporal vacuity is of a different shape; there is no foramen in the temporal arch; the whole skull is narrower and higher, and there is no palatine vacuity. Broom was probably more nearly correct in the sutures of the face; Case in those of the frontal region. Case was also apparently correct in the detection of the bone in the occipital region called by him " ? epiotic." The sutures everywhere need corroboration, and otherwise should not be accepted as certain.

Vertebræ (fig. 48): Fifteen vertebræ were found in a continuous series articulated with the skull, and their matrical attachments have been preserved in preparation. The posterior three are more or less fragmentary, and the spines of the posterior eight, which were exposed when discovered, are more or less wanting. Only a fragment of the atlas has been detected. As in most of the Pelycosauria, the first six of the vertebræ, counting the altas, may be considered as cervicals. With the seventh a much heavier rib was articulated, and it doubtless was the first thoracic vertebra. As in the different species known as *Naosaurus*, the cervical vertebræ are remarkable for their decrease in size, as also for their much shorter ventral lengths. To such an extent, indeed, are these vertebræ shortened on the under side that closely articulated the skull would be directed obliquely downward and backward. The twelfth vertebra, of much larger size, has its articular ends nearly parallel with each other, while those of the first two or three vertebræ are inclined in such an angle that the lower border is a third shorter than the longitudinal diameter on the floor of the neural canal, and is but little more than half the length of the lower border of the twelfth vertebra. Throughout the cervicals the lower, concave border is sharply keeled; further back, the lower side is more obtusely keeled. The anterior diapophyses, beginning with the axis, are more slender, but as long as those further back. In the cervical region they are directed downward and backward; posteriorly they are more transverse in position and are situated near the front end of the vertebra. The zygapophysial surfaces of the cervicals are extensive and nearly horizontal in position. The zygapophyses of this region

project nearly as much as do those of the dorsal region, notwithstanding the smaller size of the vertebræ. Like the centra, they evidently permitted not only extensive vertical flexion, but a considerable lateral one as well

The *axis* has a rather narrow spine, not expanded anteroposteriorly above, and it is but little longer than the height of the centrum. It is thin in front, much thickened and rugose behind, and is directed obliquely forward. The precise length of the spine of the next following vertebra can not be determined. It is flattened at its base, cylindrical, slender, and evidently pointed above; its extremity is directed forward at an angle of about 45 degrees with the long axis of the centrum. The spine of the fourth vertebra could not be connected with its centrum, and its length is, consequently, unknown. That of the fifth vertebra is complete, or

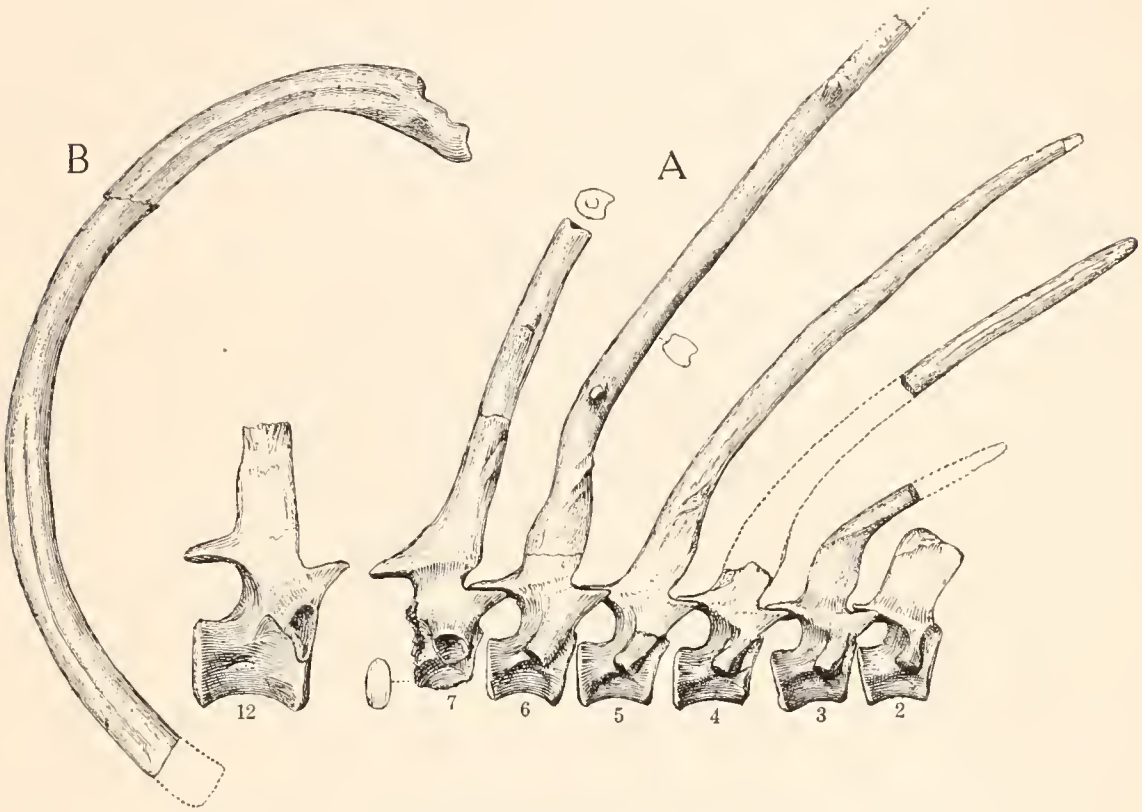

FIG. 48.—*Edaphosaurus novomexicanus*, × ½. A, vertebræ as numbered, No. 674, University of Chicago; B, rib of eighth or ninth vertebra.

practically so. It is directed upward and forward at a little less angle than the preceding ones; it is gently curved below, nearly straight above, and is obtusely pointed at its extremity. It is oval in cross-section above its flattened and rugose base, and has no lateral tubercles. The next spine is stouter, but is preserved only as far as the extremity of the one preceding it, with which it lay in close matrical contact above; it must have been at least 3 inches longer than that spine. It has two or three tubercles on its sides, in the form of rounded protuberances, projecting about a fourth of an inch. The sixth spine is still stouter, but only about 5 inches of it can be connected with the centrum. It is directed less obliquely forward, and the single pair of tubercles that this portion bears are larger. On the tenth, the base of the spine, about 3 inches in length, was recovered; it is directed

vertically. Among the many pieces of spine recovered of the posterior vertebræ, but few of which could be connected with their vertebræ, the lateral tubercles are more numerous and rather more prominent, but none could have been more than three-quarters of an inch in length.* A few of the intercentra are preserved with the vertebræ, one of which is figured, as seen from below.

Large quantities of broken ribs were secured, but only one rib could be restored completely or nearly completely; it belongs with either the eighth or ninth vertebra. Its shape and size will be sufficiently well understood from the figure (fig. 48 B). The rib seems remarkably heavy for a skull of the size of the present one.

Pectoral girdle: Both scapulæ are preserved, imperfectly. That of the right side is more complete on the lower part, that of the left on the upper. The latter has a nearly complete cleithrum in close articulation with it. The right clavicle

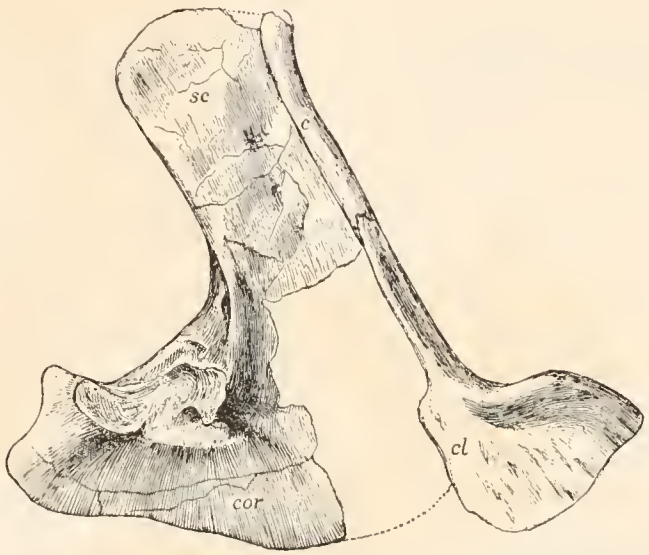

FIG 49.—*Edaphosaurus novomexicanus.* Pectoral girdle, × ⅔.
c, cleithrum; *cl*, clavicle; *sc*, scapula.

was found lying across the left scapula, and is complete. No indications of an interclavicle have been observed in the material. The right scapula is figured, with some slight additions, as also the cleithrum, reversed from the left side (fig. 49). The cleithrum is larger than has been observed in other pelycosaurs. It is a rather stout cylindrical bone, lying in close articulation along the front edge of the scapula above, thinned below for union with the clavicle, but not dilated at either extremity. The scapula is peculiar in its short, narrow, rather stout blade, and its great antero-posterior extent below. Both scapulæ are more or less crushed, and were doubtless less flat in life than shown in the figure. The large supraglenoid foramen pierces the bone back of the ridge leading to the preglenoid facet, not the outer face, as in *Dimetrodon*. A comparison of these scapulæ with that figured and described by Case † leaves little or no doubt of their generic affinity (fig. 50). Case was especially struck by the short blade of his specimen, and the great antero-

* Among the collections made by Mr. Baldwin from Poleo Creek, New Mexico, now preserved in the museum of Yale University, is a considerable fragment of a large spine, closely resembling those of "*Naosaurus*," that has elongated lateral processes.

† Journal of Geology for May 1903, page 397.

posterior extent below, characters unlike those of other scapulæ that have been observed from Texas. It undoubtedly belongs with some one of the species of *Edaphosaurus* described from Texas.

Humerus, radius: The humerus and radius of the right side, found lying closely related to the scapula, are so poorly preserved that only their chief characters can be made out. The humerus is more slender than usual; the entepicondylar foramen appears to be larger. It measures 130 mm. in length, with the least diameter of the shaft 14 mm. The radius is 80 mm. in length, or less than two-thirds the length of the humerus. In *Dimetrodon* the radius is more than four-fifths the length of the humerus.

FIG. 50.—*Edaphosaurus* sp. Scapula-coracoid of a specimen found on Coffee Creek, Texas. No. 186, University of Chicago, × ½.

CONCLUSIONS.

It will be observed that the cervical spines of the present species differ materially from those figured and described as belonging with "*Naosaurus*," in their greater anterior inclination, more slender and pointed shapes, and in the smaller development of lateral tubercles so characteristic of the genus. It is quite possible that these differences are of generic value, and that *Naosaurus* will eventually be found to be a valid genus. But this can not be determined until the type species of *Edaphosaurus* has been definitely correlated with its proper skeleton. It is more probable that the New Mexico species will prove to be the aberrant form, requiring a new generic name. If these differences really exist in the Texas species, it will be quite time enough to validate the name *Naosaurus* when the facts shall have been determined. For the present, at least, *Naosaurus* has no claims for existence.

In *E. novomexicanus*, with the neck extended horizontally, the pointed spines of the anterior vertebræ would project over the occiput. If the neck were fully

flexed, with the articular surfaces of the centra in contact or parallel, the head would be folded under the breast, the pointed cervical spines projecting directly forward. That such a posture was possible seems certain; that it was an habitual posture of the animal in life, either of offense or defense, it would be hazardous to say; and yet one can not resist the belief that it was.

The function of the greatly elongated spines in both this genus and *Dimetrodon* has been the subject of no little speculation and some very fanciful theories. There is little evidence that the spines were covered in life by a horny epidermis. They of course could not have projected freely without a nutrient covering of some kind. If, on the other hand, they were enveloped in a continuous covering, there could have been little or no motion of the vertebral column in a vertical plane, since even the slightest angle of divergence of the centra would have increased the distance between the spines enormously at the periphery. The looseness of the cervical vertebræ is almost certain evidence of the possibility of considerable flexion and that the spines throughout most of their extent could not have been connected

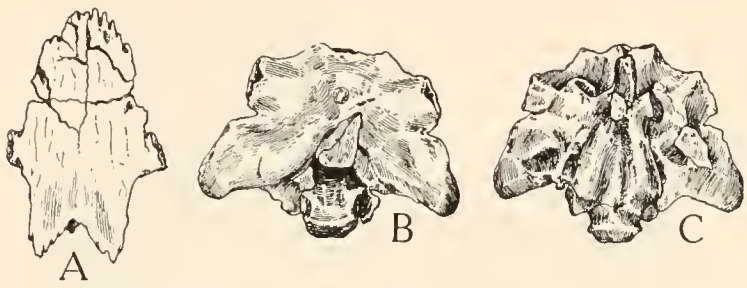

FIG. 51.—*Edaphosaurus* sp., × ½. No. 3333, University of Michigan. A, frontal; B, basioccipital, upper surface; C, basioccipital, lower surface.

by ligaments, even elastic ligaments. They must have been freely movable in the cervical region at least, probably invested by a firm skin.*

It is a curious fact that no genus of vertebrates is more commonly met with in the Texas Permian deposits than *Edaphosaurus;* isolated and fragmentary bones are found everywhere; a day seldom passes that the collector does not see one or more *Edaphosaurus* vertebræ. It is also very rarely that he finds two or more vertebræ in anatomical relationship, and hitherto there has been no record of the positive association of any other parts of the skeleton, except the pelvis. A legitimate conclusion from these facts would seem to be that *Edaphosaurus* was an inhabitant of the river plains and not of the more quiet bays and mud flats. The skeletons were broken up and brought down to the lower lands by streams and freshets. Williston has figured and described † a leg of a reptile that he suspected belongs with *Edaphosaurus*. It is peculiar in having a relatively long and slender femur and short tibia and fibula, characters invariably associated with aquatic habits in extinct reptiles. If this leg really belongs with *Edaphosaurus*, and there seems to be a similar relation between the humerus and radius, it would add to the probability that the species of *Edaphosaurus* were more or less swimming, fluviatile animals, living along the river plains and subsisting upon fresh-water mollusks and

* Case has shown that in *Chameleo cristatus* the elongated spines of the dorsal region are united by a flexible skin, with a strong thread of connective tissue running along the apices of the spines. A few scattered fibers of muscular tissue were found between the spines. This suggests the condition that existed in the long-spined pelycosaurs. (Case, Science, XXIX, p. 979.)

† American Permian Vertebrates, p. 75.

other invertebrates. Whatever may have been the use of the cervical spines in offense or defense, a like explanation will hardly account for the greatly elongated dorsal ones.

The relationships of *Edaphosaurus* and *Dimetrodon*, notwithstanding the similarity of their dorsal spines, can not be very intimate. The conclusion is irresistible that these resemblances were, for the most part at least, merely the result of convergent evolution. We know now that there were other widely different animals in the New Mexican Permian and the European Trias with greatly elongated dorsal spines. All of which render the meaning of their remarkable development still more of a problem.

NOTE BY CASE.—Further confirmation, if such be necessary, has been added to the identity of *Edaphosaurus* and *Naosaurus* by the discovery, during the summer of 1912, by Case of a nearly complete vertebral column of *Edaphosaurus* (*Naosaurus*) associated with scapula, pelvis, limb bones, and a broken and fragmentary skull indistinguishable from the type specimen of *Edaphosaurus pogonias*. Figure 51, A, B, C, shows the occipital region and frontal plate of this skull. It is of interest to add that the humerus possesses an ectepicondylar foramen as well as an entepicondylar foramen.

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